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BENTHIC STUDIES IN BUZZARDS BAY
II. THE MEIOFAUNA[1]

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ABSTRACT

During the summer of 1957 a study of the small metazoans (meiofauna), based on a series of Phleger core samples, was undertaken at three stations in Buzzards Bay, Massachusetts. The number of animals ranged from 1.69 x 10^5 to 1.86 x $10^6/m^2$, the dry weights varied from approximately 100 to 600 mg/m^2. The nematodes and kinorhynchs, which comprised between 89 and 99% of the total mieofauna, were studied in detail. The sandy localities (stations P and J) were characterized by a number of nematodes restricted to this habitat, particularly by three representatives of the genus *Odontophora* and by all representatives of the genus *Leptonemella*. The locality rich in fine deposits (station R) was characterized by the relative abundance of several nematodes, particularly of *Terschellingia longicaudata*, and the three kinorhynch species. It was possible to recognize an *Odontophora-Leptonemella* community in the sandy habitats, and a *Terschellingia longicaudata-Trachydemus mainensis* (kinorhynch) community in the silty habitat, the former being equivalent to the *Ampelisca* community, the latter to the *Nucula proxima-Nephthys incisa* community described for the macrofauna in the same area. However, these "communities" can also be considered as two ecological groups of species, the former dependent on the presence of sand, the latter on that of fine deposits, which actually live side by side, forming an intricate meshwork of faunal combinations. Each combination is determined by the relative amounts of sand and fine deposits present.

The uniformity of the nematode fauna within each station was greater than that between two different stations. Most important in determining the degree of faunal uniformity between paired samples is the similarity in their silt-clay content. However, other mechanical factors also play a role.

An analysis of the total species composition of the nematode fauna revealed that *Terschellingia longicaudata* was the most abundant species at station R, whereas at the stations P and J there were three or four equally dominant species. This is interpreted as indicating a splitting up of the sandy habitat into subhabitats. The simultaneous occurrence of closely related species in this environment further supports the conjecture.

The distribution of "buccal types" amongst nematodes is correlated with the distribution of sediments.

This is the second contribution to an investigation, initiated by Sanders (1958) which aims at as complete a picture as possible of the various vectors determining the structure and dynamics of a marine benthic community. It is concerned with the meiofauna, a term coined by Mare (1942) to characterize metazoans of medium size and which in the present paper includes the following groups: nematodes, kinorhynchs, ostracods, copepods, turbellarians, oligochaetes, halacarids, gastrotrichs and cephalocarideans. The former two groups (which together account for more than 90% of the meiofauna) are treated in detail, the others summarily without identification of species.

The area of investigation is Buzzards Bay, Massachusetts, the physiographic characters of which were described by Sanders

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(1958). The samples on which the present study is based were taken by the author and H. Sanders between July and September 1957. I am indebted to H. Sanders for extensive discussions during preparation of this manuscript and also to him and to Jay Bercaw, the skipper of the R. V. "ASTERIAS", for assistance during sampling, and to the Woods Hole Oceanographic Institution for granting me a summer fellowship.

So far, studies of submarine benthic communities have been restricted to the macrofauna. Quantitative data on the density of the meiofauna below tidal level have been supplied by Moore (1931), Krogh and Sparck (1936), Mare (1942), Bougis (1946, 1950) and Purasjoki (1947). However, in none of these cases was the meiofauna identified to species. Numerical comparisons between meiofauna and macrofauna from the same locality were made only by Krogh and Sparck and by Mare. Recently, a very complete and thorough study of the sublittoral nematode fauna of the Bay of Kiel has been undertaken by Gerlach (1958) who delimited only qualitatively the fauna of different types of substrate. This holds also for Filipjev's classical work on the nematode fauna in the vicinity of Sebastopol (Filipjev 1918/21), for the author's investigation into the nematode fauna off the Chilean coast (Wieser 1958), and for the few studies dealing with the other meiofauna groups, *e.g.* ostracods (Elofson 1941), copepods (Lang 1948) and turbellarians (Riedl 1954).

METHODS

Collecting

The samples were taken with a Phleger core sampler, the plastic tubes of which have an inner diameter of 3.4 cm, circumscribing an area of 9.07 cm^2. In this paper, however, the area will be considered equivalent to 10 cm^2. In sand the core sampler did not work too well, but its efficiency could be slightly improved by attaching a brass core catcher to the opening of the tude. Only undisturbed cores were used. Samples were taken at three stations, the average sediment composition of which had been established earlier by Sanders (1958, Figure 1, Tables 1, 2). Station P comprised well sorted sand with little silt-clay, station J poorly sorted sand with much silt-clay and station R silt-clay with little sand. One sample, termed RA–1, was taken at station R but resembled a J-sample in appearance and sediment composition. In all, 5 single and 7 pairs of replicate samples were taken (Table 1). With each single and each pair of replicate samples an additional sample for sediment analysis was collected. This procedure introduced an uncertainty factor since the sample on which the faunal and the sediment analyses were based did not come from the same spot of substratum. This was not considered serious since the general sediment composition of the stations had already been established by Sanders, making it easy to distinguish macroscopically between the three types of substrate, and since the scope of the present investigation was to study the general structure of the meiofauna populations at the three stations rather than to elucidate in a detailed manner sediment-animal relationships.

The plastic tube containing the sample was taken to the laboratory, the water was siphoned off and the core was pushed upwards by means of a rubber plunger. The upper 7cm of the core, which had been shown previously to contain almost all the animals (see also Moore 1931, Mare 1942), were cut off and put into a 500 cc graduated cylinder which was then filled with filtered sea water and thoroughly shaken. After allowing sand to settle, the supernatant was poured through a screen with a mesh width of 160μ. The water with the fine particles that went through the screen was caught in a bucket. This procedure was repeated several times and resulted in separating the sample into three fractions: 1) the sand fraction in the cylinder 2) the medium fraction retained by the screen, and 3) the fine fraction that passed through the screen and was caught in the bucket.

Fraction 1 was discarded since repeated checks showed that a very thorough shaking

TABLE 1. *Grain size distribution and depth of samples taken in Buzzards Bay. Brackets unite samples which are considered replicates (see text)*

Sample No.	Date	Depth (m)	Grain size in mm Sand >1.0	1.0–0.5	0.5–0.25	0.25–0.12	0.12–0.05	Silt-clay <0.05	Ave. silt-clay content
P-1	7/8	18	0.2	0.4	5.9	81.4	5.8	6.3	
P-2	7/19	18	0.2	1.6	7.7	59.6	10.3	20.6	
P-3	8/9	18–20	0.1	0.6	8.6	78.6	6.6	5.5	
P-4	—	—							11.8
P-5	8/30	30	2.8	6.6	3.17	39.1	5.1	14.7	
P-6	—	20							
RA-1	7/12	18	5.1	13.5	30.1	16.1	8.2	27.0	
J-1	7/12	12	7.3	30.4	31.1	18.4	6.5	6.3	
J-2	—	—							
J-3	8/2	12	7.5	26.1	24.3	6.7	7.4	28.0	30.0
J-4	—	—							
J-5	8/16	12	1.9	7.4	9.9	4.8	17.7	58.3	
J-6	—	—							
R-1	7/12	18	0.2	0.3	0.5	1.3	13.1	84.6	
R-2	7/29	18	0.1	0.1	0.5	1.6	17.4	80.3	
R-3	—	—							79.7
R-4	8/21	18	0.2	0.3	1.3	3.5	20.4	74.3	
R-5	—	—							
R-6	9/12	18	0.2	0.2	0.7	2.3	14.4	82.2	

tears loose all the animals and puts them into the supernatant. Fraction 2 was examined under the microscope, the animals being picked out and counted. Sometimes it was found necessary to divide this fraction and to examine only ½ or ¼ of it, extrapolating the results. The bucket with fraction 3 was left to stand in running sea water or in the refrigerator until the examination of fraction 2 had been completed. Then the water in the bucket was thoroughly stirred and 4 or 5 aliquots taken with a large pipette. Each aliquot was put into a Petri dish and allowed to settle. The fine deposits form a thin layer in which even very small nematodes can be seen under the microscope at strong illumination as long as they are alive and wriggle actively. The number of animals was extrapolated to the total volume of water present in the bucket.

Weight determinations

No meaning can be attached to the wet weight of small animals determined by direct weighing since evaporation through the body wall takes place too rapidly to allow the definition of a stable state. Thus dry weights only should be used. However, in order to allow comparisons with the macrofauna where very often only the wet weight is given, it would be desirable if wet weight values of the meiofauna were also available. It is fortunate in this respect that the most abundant meio-animals, the nematodes, due to their nearly cylindrical shape, lend themselves to weight determinations on the basis of volume and specific gravity measurement.

The nematodes before preparation were stretched in an oven at about 48°C, then fixed in 4% formaldehyde and transferred into pure glycerine by the evaporation method, a process which should take several days. The nematodes were mounted on slides, using glass rods or short pieces of nickel-chromium (Capstick 1956), tantalum or some other wire to support the coverslip. If the transfer into glycerine and the selection of the supporting rods is carried out carefully no significant shrinking or squashing of the animals occurs. At this stage the volume of the nematodes was determined by calculating $L \times (W/2)^2 \times \pi$, L being the length, W the body width at the middle of

TABLE 2. *Estimates of the ratio of dry weight to wet weight for various nematodes*

Number weighed	Species	Weight in mg			
		Wet	Dry	Dry/Wet × 100	Type of Balance
124	*Enoplus communis*	5.44	1.42	26.1	quartz helix
28	*Enoplus communis*	1.48	0.41	27.7	quartz helix
48	*Enoplus communis*	2.14	0.60	28.0	analytical
73	*Enoplus* sp., *Sphaerolaimus dispar*, *Anticoma litoris*, etc.	2.43	0.50	20.6	analytical
49	*Metoncholaimus pristiurus*	0.725	0.196	27.0	quartz helix

the oesophagus. In species with a very long filiform tail, the length of the animal was taken from the anterior end to the end of the conical portion of the tail. In most species the diameter at the middle of the oesophagus corresponds reasonably well to the diameter of the imaginary cylinder, the volume of which is equivalent to that of the nematode. The same assumption was made by Nielsen (1951), who compared the results achieved by this method with those of another method and found good agreement. The values obtained do not differ significantly from those obtained with Andrassy's formula $a^2b/1.7$, in which a is the *maximum* width and b the length of the nematode (Andrassy 1956).

The volume multiplied by specific gravity gives the wet weight. The specific gravity of the marine nematode *Enoplus communis* Bast. was determined by flotation in a series of mixtures of kerosene and bromobenzene (suggested by Dr. J. Kanwisher). A value of 1.13 was obtained and taken as characteristic of all marine nematodes. Nielsen found a value of 1.02 and Andrassy of 1.084 for fresh water and terrestrial nematodes.

As every specimen could not be measured, an average volume was computed for the adults of each species; the juveniles were assumed to measure half that much. From the number of nematodes identified (ranging from 59 to 233 per sample) an average weight per specimen was calculated which, multiplied by the number of animals counted, gave the wet weight per sample or per 10 cm^2.

The mean wet weight of one nematode ranged from 0.0012 mg in sample R–3 to 0.0041 mg in sample RA–1, agreeing well with Mare's figures of 0.0017 to 0.003 mg which she determined by direct weighing of batches. This seems to invalidate the statement above that no meaning can be attached to the wet weight of small animals determined by direct weighing. However, as will be shown below, there is reason to assume that Mare's samples did not include the very small nematodes and that her values refer to the dry rather than to the wet weight of medium sized and large nematodes. The individual wet weights of the Buzzard Bay nematodes ranged from 0.0002 mg (several species) to 0.138 mg (*Enoplus behringicus*).

To determine the dry weight of nematodes, batches were weighed on an analytical balance (Becker, 0.1 mg) or on a "Misco" quartz helix (manufactured by Michrochemical Specialties Co., Berkeley, California) with a sensitivity of 1 mm per 10 mg. The specimens whose wet weight had been determined previously by the volume method were preserved in formalin, rinsed and oven dried. The weighing on the quartz helix was carried out by Dr. R. Conover. The results are given in Table 2. From these data a mean dry weight/wet weight ratio of 25% was adopted and the wet weight values per sample were converted into dry weight values accordingly (Table 4).

Representatives of all other meiofauna groups were preserved in formalin, rinsed and weighed in oven dried condition with the quartz helix. These weights are listed in Table 3. An average dry weight of 0.003, 0.018 and 0.0017 mg for one kinorhynch, one ostracod and one copepod respectively was adopted for these groups. The cope-

TABLE 3. *Average weights of meiofaunal groups*

	Number of specimens weighed	Total weight (mg)	Average weight per specimen
Kinorhyncha			
Pycnophyes frequens	50	0.167	0.0033
Ostracoda			
representatives of three species	12	0.221	0.018
Copepoda			
representatives of two species	20	0.035	0.0017

pods weighed by Mare (1942) possessed an average individual (wet?) weight of 0.0024 and 0.005 mg.

RESULTS

The numerical results of the present study are given in Table 4. The total numbers of specimens vary between 1.69×10^5 and $1.86 \times 10^6/m^2$, the calculated dry weights between 100 and 600 mg/m^2.

The average distribution of nematodes and kinorhynchs at the three stations investigated is set out in Table 5. Rare nematode species are not listed but will, together with the more abundant ones, be described in a later publication.

There is a considerable number of species confined to the sandy stations, amongst them some of the more abundant forms such as *Odontophora pugilator, O. papusi* and *Anticoma litoris.* Three of the four species of *Odontophora* and all three representatives of the genus *Leptonemella,* together with their associated blue-green algae, (*cf.* Wieser 1959c) are restricted to the sandy habitats. Few species occur at station J alone, the most abundant of these being *Nudora lineata. Neochromadora pistillata* is most abundant at station J although it also occurs at stations P and R. The soft bottom habitat, station R, can be characterized by the relative abundance of certain species, particularly of *Terschellingia longicaudata,* followed by *Odontophora loffleri, Sabatiera ornata, S. hilarula, S. vulgaris, Sphaerolaimus dispar* and all the kinorhynchs.

An analysis of the total species composition of the nematode fauna is shown in Figure 1. At the fine deposit station (R) the dominance of the most abundant species, *Terschellingia longicaudata,* is quite pronounced, whereas at the sandy stations J and P three or four equally dominant species occur. Station R also carries fewer species than either P or J.

The question may arise as to what extent the sampling sites represent homogeneous habitats and whether the animals living in these habitats represent homogeneous populations. The degree of uniformity, or affin-

TABLE 4. *Numbers and dry weights of the meiofauna groups in Buzzards Bay samples. The numbers are given per 10 cm^2, the dry weights in mg/m^2*

Numbers/10 cm^2:	P-1	P-2	P-3	P-4	P-5	P-6	RA-1	J-1	J-2	J-3	J-4	J-5	J-6	R-1	R-2	R-3	R-4	R-5	R-6
Nematoda	350	250	400	300	550	335	150	600	650	225	150	190	300	250	760	500	690	790	1800
Kinorhyncha			1	1	2		1	2	2	2	5		5	8	16	7	16	12	39
Ostracoda	4	25	?	2			6	1	1	2	2	1	5	16	3	4	1	6	4
Copepoda		4		4	4	6		10	6	6	7	4	11	2	8	2	3	9	12
Turbellaria		1	1	3	2		4		2	4	5	7	7		2	1	2	6	6
Halacaridae		2				1	3	7	3								1		
Gastrotricha							5												
Cephalocaridea		2																	
Total	354	284	402	310	558	342	169	620	664	239	169	202	328	276	789	514	713	823	1861
% nematodes	99	89	99	97	99	98	89	97	98	94	89	94	91	90	96	97	97	96	96
mean number of meiofauna/m^2			380,000							340,000						838,000			
mean number of macrofauna/m^2 (Sanders 1958):																			
total			12,576							5,455						6,068			
deposit feeders			3,084							2,836						5,545			
weights mg/m^2:																			
Nematoda	145	130	139	145	230	158	152	475	375	90	82	78	95	110	268	149	270	331	—
Kinorhyncha			3	3	6		3	6	6	6	15		15	24	48	21	48	36	—
Ostracoda	72	450	?	36			108	18	18	36	36	18	90	288	54	72	18	108	—
Copepoda		7		7	7	10		17	10	10	12	7	19	3	14	3	5	16	—
rest (estimated)		9	1	3	2	2	20	14	8	4	5	7	7		2	1	4	6	—
Total	217	596	143	194	245	170	283	530	417	146	150	110	226	425	386	246	345	497	—

TABLE 5. *Mean abundance of nematode and kinorhynch species (rare species not included) at stations P, J and R, in Buzzards Bay, Massachusetts. 'Frequency' refers to number of samples in which a given species was found (based on 6 samples at stations P and R respectively, 7 samples at Station J). * = less than 0.3%*

	Station P		Station J		Station R	
	Per cent abundance	Frequency	Per cent abundance	Frequency	Per cent abundance	Frequency
Nematoda						
Odontophora pugilator Wieser	9.6	6/6				
Odontophora calcarea Wieser	1.8	5/6				
Synonchiella bifaria Wieser	0.8	4/6				
Chromaspirina arietina Wieser	1.1	3/6				
Latronema macramphida Wieser	0.4	3/6				
Pomponema mirabilis Cobb	1.1	2/6				
Paracanthonchus spectabilis Allgen	1.1	2/6				
Odontophora papusi Wieser	9.7	6/6	5.9	7/7		
Anticoma litoris Chitwood	11.8	6/6	1.1	2/7		
Leptonemella aphanothecae Gerlach	2.2	6/6	*	1/7		
Viscosia sp.	3.2	5/6	*	1/7		
Mesacanthion sp.	1.6	5/6	*	2/7		
Leptonemella pellita Wieser	1.8	3/6	*	2/7		
Viscosia glabra (Bastian)	1.0	3/6	0.4	3/7		
Leptonemella cincta Cobb	0.6	3/6	*	1/7		
Monoposthia costata (Bastian)	1.2	5/6	1.8	4/7		
Halalaimus simiferus Wieser	*	3/6	*	2/7		
Laimella quadrisetosa Chitwood	1.0	4/6	1.3	6/7		
Dichromadora cephalata (Steiner)	0.7	3/6	*	1/7		
Cobbia crenata Wieser	0.7	2/6	0.5	1/7		
Theristus multisetosus Wieser	0.6	3/6	1.1	4/7		
Bathylaimus tenuicaudatus (Allgen)	0.5	2/6	0.4	1/7		
Pareurystomina typicum Micoletzky	*	2/6	0.6	3/7		
Theristus sp.	0.6	1/6	0.6	3/7		
Dorylaimopsis metatypicus Chitwood	11.0	6/6	7.6	7/7	4.4	3/6
Neochromadora poecilosoma (de Man)	2.3	5/6	0.8	2/7	1.4	3/6
Neochromadora pistillata Wieser	2.3	5/6	9.5	7/7	1.8	4/6
Desmodora cephalata Cobb	0.8	5/6	1.3	4/7	1.5	5/6
Sabatiera hilarula (de Man)	1.4	5/6	1.2	5/7	4.3	6/6
Terschellingia longicaudata de Man	1.0	5/6	8.8	6/7	29.6	6/6
Desmodora devestita Wieser	0.7	4/6	1.9	6/7	*	2/6
Odontophora löffleri Wieser	0.6	4/6	1.2	3/7	7.7	6/6
Axonolaimus spinosus (Butschli)	1.6	3/6	*	1/7	*	1/6
Actinonema pachydermatum Cobb	1.0	3/6	0.6	3/7	3.6	5/6
Cervonema mediocris Wieser	0.5	3/6	0.8	3/7	1.3	4/6
Chromaspirina ciliata Wieser	0.4	3/6	1.1	4/7	1.4	4/6
Sabatiera ornata Ditlevsen	0.8	3/6	1.8	4/7	5.6	5/6
Oncholaimus sp.	0.7	3/6	*	3/7	0.5	3/6
Sabatiera tenuicaudata (Bastian)	1.0	3/6	0.5	4/7	0.5	1/6
Rhabdodemania minima Chitwood	1.1	3/6	0.8	1/7	2.0	6/6
Oxystomina elongata (Buetschli)	*	2/6	*	1/7	0.6	4/6
Metalinhomoeus additus Wieser	0.4	2/6	*	1/7	2.2	5/6
Halichoanolaimus robustus (Bastian)	*	2/6	1.1	4/7	1.4	4/6
Tripyloides gracilis (Ditlevsen)	0.5	2/6	1.5	5/7	*	1/6
Metalinhomoeus setosus Chitwood	0.7	3/6	0.6	3/7	0.6	4/6
Sabatiera vulgaris (de Man)	*	2/6	2.1	2/7	3.5	3/6
Paironus sandersi Wieser	0.6	2/6			1.0	4/6
Microlaimus sp.	*	1/6	0.4	3/7	0.5	2/6
Paramonhystera biforma Wieser	*	1/6	*	2/7	1.3	4/6
Chromadora axi Gerlach	*	1/6	1.1	4/7	*	1/6

TABLE 5. *(Continued)*

	Station P		Station J		Station R	
	Per cent abundance	Frequency	Per cent abundance	Frequency	Per cent abundance	Frequency
Hypodontolaimus patagiatus Wieser	*	2/6	0.7	3/7	*	1/6
Linhomoeus buculentus Wieser	*	2/6	1.0	3/7	1.7	3/6
Sphaerolaimus dispar Filipjev	*	1/6	2.7	5/7	3.5	5/6
Oxystomina beta Wieser	*	2/6	1.1	4/7	*	1/6
Lauratonema originale Gerlach	*	1/6	0.4	2/7	*	1/6
Monhystera parva (Bastian)	*	2/6	*	1/7	0.4	2/6
Neochromadora attenuata Gerlach	*	1/6	0.5	3/7	0.4	2/6
Metalinhomoeus dimorphus Wieser	0.4	2/6	1.5	5/7	0.9	2/6
Comesoma pararenae Wieser			0.8	3/7		
Nudora lineata Cobb			3.2	4/7		
Enoplus behringicus Filipjev			0.7	2/7		
Paramonhystera mystacoderma Wieser			1.5	2/7		
Linhomoeus iniquus Wieser			0.5	3/7		
Halalaimus sp.			0.6	3/7		
Filipjevinema potor Wieser			4.6	6/7	0.7	1/6
Sphaerolaimus margaritatus Wieser			0.5	3/7	*	1/6
Paralinhomoeus sp.			0.5	3/7	*	1/6
Sphaerolaimus nefastus Wieser			*	1/7	0.7	3/6
Pareurystomina flagellicaudata Stekh.			*	2/7	*	2/6
Prochromadorella sp.			0.4	2/7	1.0	3/6
Eleutherolaimus stenosoma (de Man)			*	1/7	1.0	4/6
Halalaimus anulatus Wieser					1.3	2/6
Number of rare species	45		35		21	
Total number of species	103		98		63	
Number of identified specimens	786		821		759	
Kinorhyncha						
Trachydemus mainensis Blake	*	1/6	0.3	4/7	0.6	6/6
Pycnophyes frequens Blake			*	4/7	0.4	6/6
Echinoderella remanei Blake			*	2/7	*	3/6
larvae	*	2/6			*	3/6
remaining groups of meiofauna	2.7%		5.2%		3.7%	
total number of counted specimens	2250		2391		4976	

ity, of a certain population can be established in the following way. The abundance of each species is expressed as a percentage of the total population. The percentages, or abundance values, of each species in two samples are compared and the smaller of the two is taken as the "common abundance value." The common abundance values are added up and the result represents in a quantitative way the faunal element common to the two samples. Thus, if three species, A, B and C, constitute the following percentages in two samples:

	sample I	sample II
species A	15%	76%
species B	27%	0
species C	58%	24%

The common abundance value for species A is 15%, for species B zero, and for species C it is 24%, which means that the two samples have 39% of their fauna in common.

If all possible pairs of samples are compared we arrive at a pattern of values which gives an idea of the degree of uniformity of the population from which the samples were derived. This is the so-called "trellis

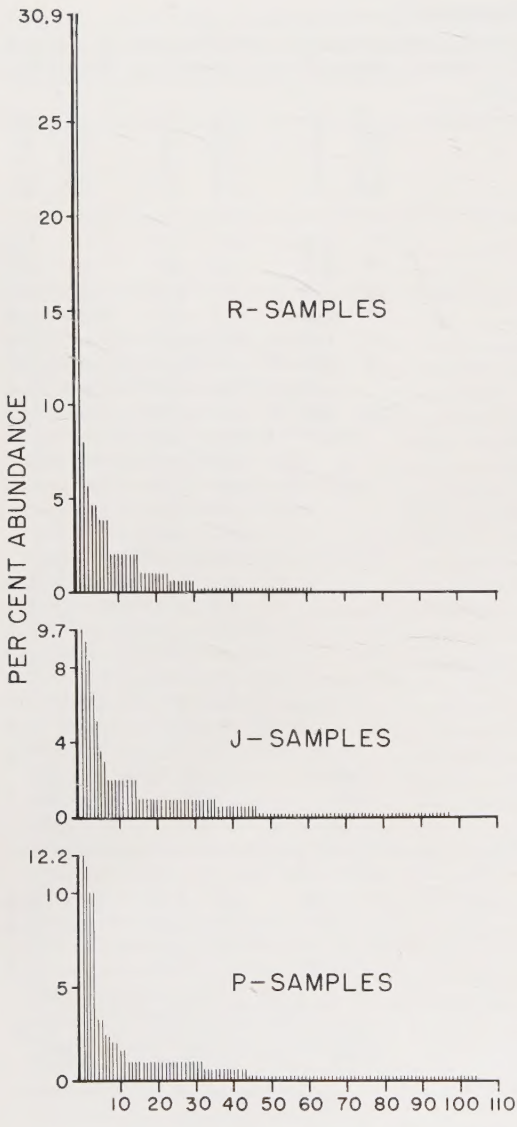

FIG. 1. Average species composition of the nematode fauna at the three stations studied. Each line represents one species, its height indicating the average abundance of the species in per cent of the total nematode population at the respective station.

diagram" which has been used widely by Scandinavian workers for delimitating communities of terrestral animals (*e.g.* Tenkonen 1944). The method has been criticized by Macfadyen (1954) but it seems to the writer that this criticism does not apply to the animal populations dealt with here. For a further discussion of the method see Sanders (1960).

Such an analysis of the nematode fauna at the three stations is shown in Figure 2. It is apparent that the uniformity of the fauna within each station is greater than that of two different stations. The two extreme stations, P with an average silt-clay content of 11.8% and R with a corresponding value of 79.7%, have relatively little in common, while station J with 30% silt-clay content assumes an intermediate position having about as much in common with P as with R.

DISCUSSION

Numbers

The most striking fact emerging from Table 4 is the dominance of the nematodes, which constitute between 89 and 99%. This is probably a feature characteristic of all marine shallow water substrates. If the data given in the literature are examined (Table 6) we find the nematodes varying between 43 and 100%.[1] However, the lower values are most probably due to sampling errors. In the present investigation both the material retained by and that passing through a 160μ screen was examined and it was found that between 10 and 60% of the living nematodes may go through the screen. Bougis (1946) estimated that with preserved material about 20% of the nematodes will pass a 200μ screen. Moore (1931), Mare (1942) and Purasjoki (1947) who worked with fresh material and counted only the animals, retained by a 200μ or a 100μ screen, probably missed considerable portions of the nematode populations.

In general it can be said that the samples rich in silt and clays (R) supported a larger number of meiofaunal animals than those poorer in fine deposits (J and P). The total macrofauna shows the opposite relationship, due to the abundance of filter

[1] These values refer to the meiofauna as defined in the first paragraph, which means that polychaetes are not included. Consequently, this group has been omitted in Table 6 and the figures given by the various authors have been recalculated.

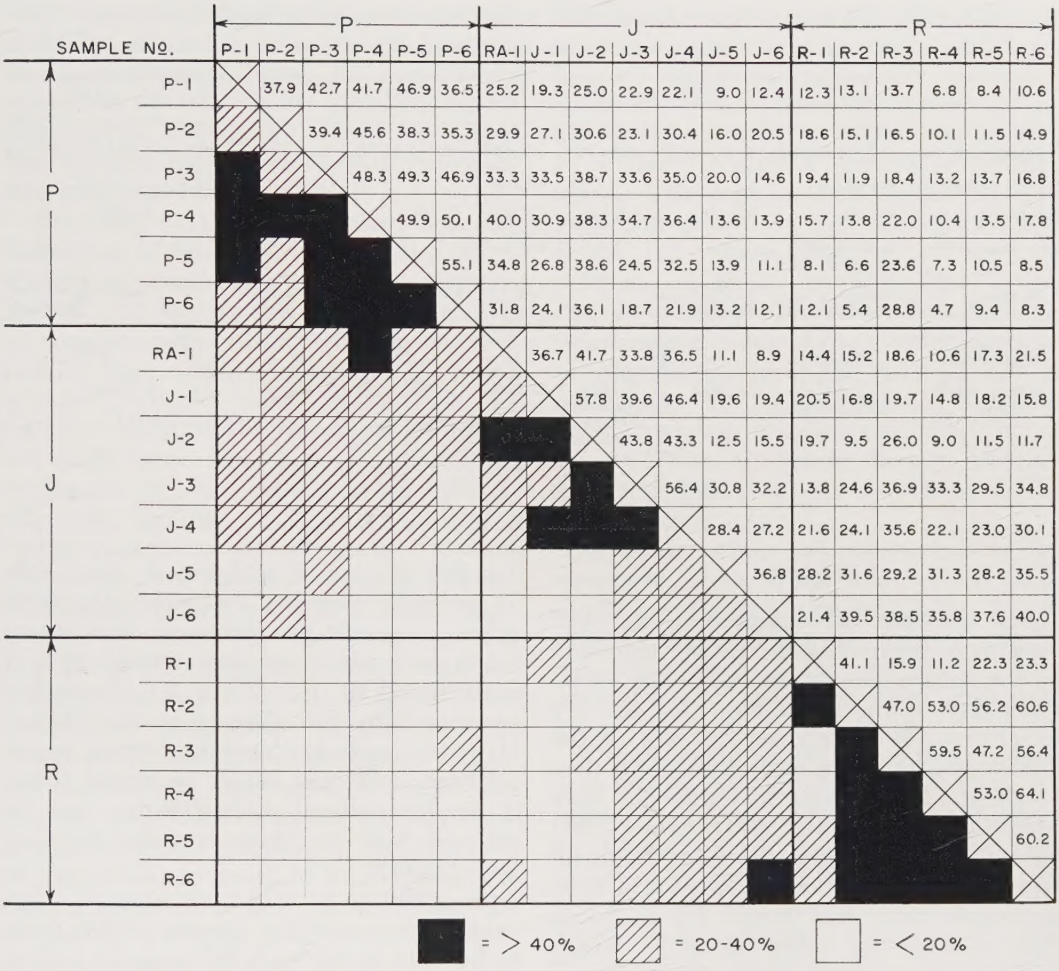

FIG. 2. "Trellis diagram" illustrating the degree of uniformity of the nematode fauna at the three stations investigated. Each number (and square) indicates the nematode fauna common to a pair of samples (see text).

feeders at station P (Sanders 1958). However, if we select the deposit-feeding component of the macrofauna the relationship displayed by the meiofauna is exactly paralleled (Table 4).

In comparing meio- and macrofauna, we find that the former exceeds the latter by a factor of 30–100, values around 100 probably being more common than lower ones.

The numbers of larger animals brought up by the Phleger core-samples conform well with the numbers obtained by dredging. For example, in six samples from R, the lamellibranch *Nucula proxima* was represented by 0, 2, 2, 3, 4 and 5 specimens respectively, yielding an extrapolated mean value of $2.5 \times 10^3/m^2$, while Sanders (1958, Table 6) reports a mean of $3.3 \times 10^3/m^2$ from the same station.

The meiofauna densities reported from various parts of the oceans are in good agreement with each other (Table 6), particularly if we take into account that the figures given by Moore and by Mare probably are too low. The low values found by Krogh and Sparck (1936) and by Purasjoki (1947) might be due to either the sampling method, or to the impoverishment of the brackish water habitats on which these authors worked.

TABLE 6. *Summary of quantitative results pertaining to the subtidal benthic meiofauna*

		Wieser (this paper)	Bougis 1946	Bougis 1950	Mare 1942	Moore 1931	Krogh & Sparck 1936 a)	Krogh & Sparck 1936 b)	Purasjoki 1947
meiofauna	specimens/m²	1.7–18.6×10⁵	4–11.3×10⁵	6.6×10⁵	1.5×10⁵	1.7–3.5×10⁵	5.1×10⁴	7×10⁴	1.0–10.0×10⁴
	wet weight/m²	0.4–2.5 g			1.15 g		7.1(!) g	7.0(!) g	
	% nematodes	89–99	70–80	66–76	59–66	75–91	92	100	43–83
macrofauna/m²		5–13 × 10³ (Sanders 1958)			2.3 × 10³				
locality		Buzzards Bay, Massachusetts	Bay of Lyon, Mediterranean		near Plymouth, England	Clyde Sea, Scotland	Oresund, Denmark		near Tvärminne, Finnland
							reduced salinity		
depth (m)		12–30	30		45	24	26	54	9–55
screen, treatment		<, > 160μ, fresh material	> 200μ preserved, stained material	> 100μ corrected for loss of small anim.	> 100μ fresh material	> 200μ	< 500μ fresh material		> 100μ

Weights

For the sake of comparison, the wet weights of the meiofauna can be calculated on the volume determinations of the nematodes and on the assumption that the dry weight of the other groups is 25% of the wet weight. A range of 0.4–2.5 g/m² is then obtained. In previous investigations only Mare (1942) and Krogh and Sparck (1936) have given wet weight values for the meiofauna. Mare's value of 1.15 g/m² is in good agreement with that found for Buzzards Bay, whereas the values given by Krogh and Sparck are much higher. However, in the latter paper an average weight of 0.1, 0.75 and 0.45 mg is assigned to one nematode, one turbellarian and one infusorian respectively, which as already noted by Mare is impossible. It is suggested that somewhere in the calculations an error of at least one order of magnitude must have occurred.

Species Distribution

In general it can be said that the sandy stations, P and J, are characterized by a number of stenotopic species, that is, species which do *not* occur at R. On the other hand, nearly all species occurring at R, also occur at J or P or both, but sometimes in much smaller numbers. This might reflect the distribution of the sediments. The 5 to 20% silt present at station P (see Table 1) probably provides sufficient interstitial space to permit the existence of a scarce "siltfauna," while the approximate 20% of sand found at R will be so thoroughly smothered by the abundance of silt and clay that animals dependent on a sandy substrate will only rarely be found there. A similar pattern of distribution can be inferred from the data provided by Gerlach (1958).

In addition to these two groups there exist many eurytopic species which seem to be able to thrive both in sandy and in silty substrates; the most important of these is *Dorylaimopsis metatypicus*.

The mechanical composition of the substrate is important in determining the distribution of the macro- and meiofauna (Sanders 1958, Webb and Hill 1958, Wieser 1959a). However, the sediment composition might effect these two faunal components somewhat differently. In one sense, the species assemblage listed for station P might be the meiofauna equivalent of the *Ampelisca* community reported by Sanders (1958) as being typical of sandy substrates in Buzzards Bay, and the species assemblage listed for station R might be equivalent to the *Nucula proxima-Nephthys incisa* community of fine deposits, with station J occupying an intermediate position between these two types. If so, the meiofauna

equivalent of the *Ampelisca* community could be called the *Odontophora-Leptonemella* community, and the meiofauna equivalent of the *Nucula proxima-Nephythys incisa* community could be called the *Terschellingia longicaudata-Trachydemus mainensis* community.

However, as previously mentioned, the meiofauna of Buzzards Bay can also be regarded as consisting of three ecological groups: 1) species with affinity to sand, 2) species with affinity to fine deposits and 3) more eurytopic species. The fauna at each particular point of Buzzards Bay will be determined by the degree of mixing of sands and fine deposits, the three ecological groups actually living side by side and forming an intricate meshwork rather than the mosaic of patches, to which the community pattern usually is likened. The intricacy, and variability, of the meshwork is due to the fact that animals with a mean diameter of 30 μ and a mean length of 1.2 mm can exploit minute changes in the mechanical composition of the substrate much more thoroughly than the members of the macrofauna, and thus give rise to very gradual transitions from one extreme type of distribution to the other. The sensitivity of the nematode fauna to small changes in the composition of the substrate was also noticed by Gerlach (1958, p. 65).

Summarizing, it can be said that the meiofauna found in any sample represents a transect through at least three ecological groups of species. Each sample can be characterized by the degree of dominance of species belonging to these ecological groups, but to call any of them a "community" seems to be a misapplication of this term. On the other hand, to call the whole mixture a community would gloss over the fact that it consists of ecologically different components which combine to create a subtly graded series of faunal assemblages.

Too few data are available in the literature to correlate, even in a general way, the distribution of the shallow water meiofauna with the distribution of sediment types. Drawing on the studies by Gerlach (1950, 1958), Cobb (1920, 1933), and Wieser (1958a) it is suggested that the following nematode genera which occur at Buzzards Bay are characteristic of sandy substrates: *Synonchiella, Latronema, Pomponema, Leptonemella, Laimella,* to which may be added a great number of species of *Odontophora. Odontophora* is also one of the most important genera on the beaches of Puget Sound; (*cf.* Wieser 1959b).

Wieser (1958a), Gerlach (1958) and Filipjev (1918) show that *Terschellingia longicaudata* is one of the most characteristic representatives of the subtidal silt- or mudfauna. To this category can be added a great number of species of *Sabatiera* (*cf.* Wieser 1958a, b) *Sphaerolaimus, Metalinhomoeus,* and most representatives of the order Kinorhyncha.

In deeper water the composition of the nematode fauna of the soft bottom seems to change. Investigations in Chile (Wieser 1958a) suggest that at greater depths *Sabatiera* becomes the dominant genus, while *Terschellingia* and other linhomoeid genera decrease in importance.

The degree of uniformity of two samples, as defined above and shown in Figure 2, depends to a certain extent on the difference in silt-clay content between the two samples. If, choosing only one of each pair of replicates, the samples represented in Figure 2 are arranged according to their difference in silt-clay content, it can be inferred from Figure 3 that the faunal element common to two samples increases with decreasing difference in silt-clay content. It is nearly true to say that, if the difference in silt-clay content between two samples amounts to more than 40%, the two samples will have not more than 20% (mean 15%) of the fauna in common. If the difference in silt-clay content is less than 30%, the two samples will have more than 20% (mean 35%) of the fauna in common.

On the other hand, the variability of the values is considerable. This may be partly due to the fact that sediment and faunal analyses were carried out on replicate instead of the same samples, but it may also be because the faunal composition of a sample is not always, and not entirely, determined by its silt-clay content. If we

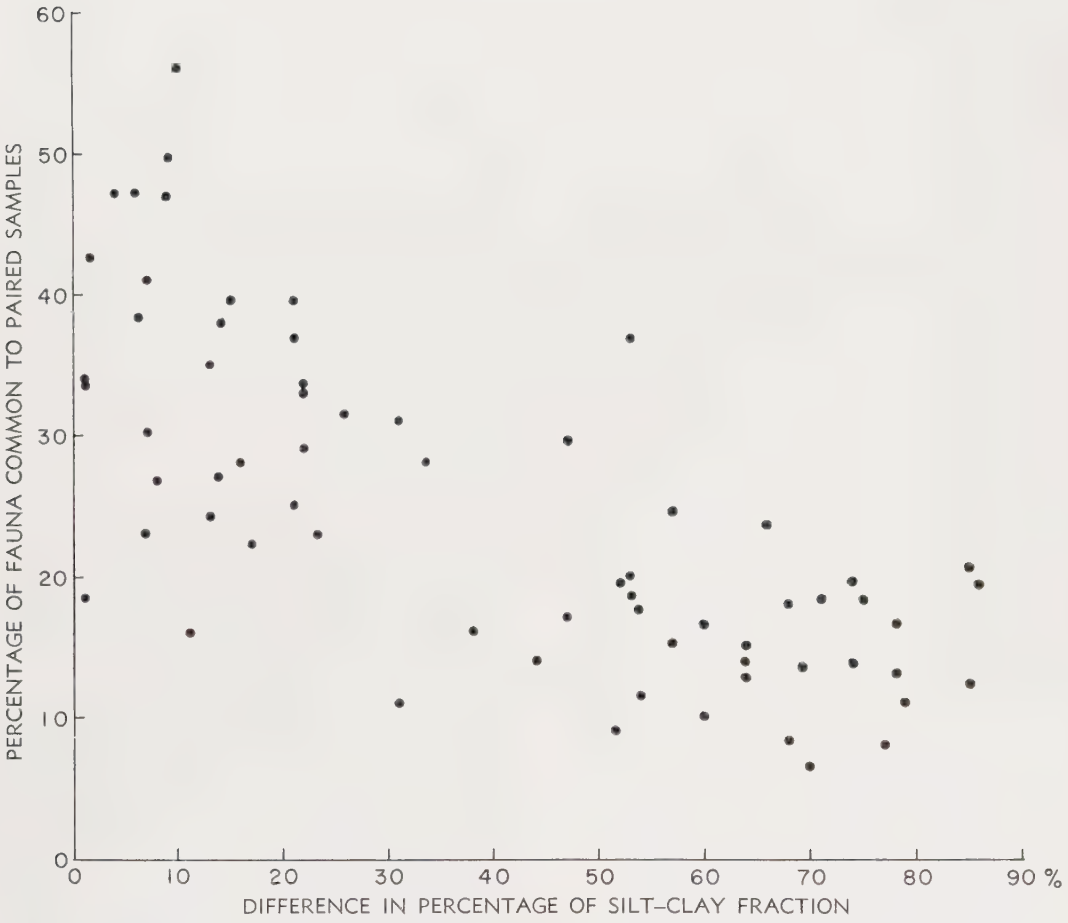

FIG. 3. Showing the dependence of the degree of uniformity of two samples on the sediment composition. The degree of uniformity (ordinate) is expressed as the per cent of the nematode fauna common to two samples, the sediment composition (abscissa) as the difference in the per cent silt-clay content between the two samples.

compare samples P–1 and J–1, we find that they have the same silt-clay content of 6.3% (Table 1), whereas the uniformity of their meiofauna is not high (19.3%). On closer inspection, however, it emerges that apart from the silt-clay content, the sediment composition of these two samples is quite different, P–1 representing a well-sorted fine sand habitat and J–1 a poorly-sorted medium or even coarse sand habit. It is conceivable that the lack of faunal conformity between the two samples has its basis in these differences of sediment composition. A similar effect of the sorting coefficient of the substrate on the fauna has been noted by Sanders (1958) with regard to the distribution of filter feeders.

Species dominance

Following Gause (1934) it has become generally accepted that two species with the same ecological requirements cannot live together in the same habitat; one of the two species will inevitably eliminate the other. Gause's contention was based in mathematical and experimental grounds, and in order to apply it to the natural environment

TABLE 7. *Per cent abundance of closely related species of nematodes in Buzzards Bay*

	P-1	P-2	P-3	P-4	P-5	P-6	RA-1	J-1	J-2	J-3	J-4	J-5	J-6	R-1	R-2	R-3	R-4	R-5
Odontophora pugilator	18.5	2.9	5.3	6.2	13.3	12.9	6.6	4.5	11.2	10.5	9.0	1.7	2.0					
O. papusi	10.8	6.8	14.4	12.3	8.5	7.1												
O. calcarea	2.3		2.6	1.5	2.4	2.9												
O. löffleri	0.8	1.9	0.5		0.6						1.1	5.1	2.9	13.9	4.3	4.5	11.8	6.2
Leptonemella pellita	8.5	1.3		1.5				0.5	0.6									
L. aphanothecae	4.6	3.9	1.1	1.5	1.2	1.4		1.0										
L. cincta	1.5			0.8		1.4		1.0										
Neochromadora pistillata	2.3	3.9	1.6	3.8	1.2		14.5	11.9	20.1	8.7	9.0	1.7	1.0	3.5			0.7	2.7
N. poecilosoma		1.0	6.4	3.1	1.2	2.9		2.0	4.5						0.6		2.2	
N. attenuata						1.4		0.5				1.7	2.0				1.5	0.7
N. sp.								2.5	0.6									
Sabatiera hilarula	3.1		2.1	2.3	0.6		1.3	1.0	1.1	0.9	4.5			13.9	1.9	0.7	0.7	1.4
S. ornata		1.9	1.6	1.5						6.1	2.2	3.4	2.0	0.9	4.3	7.1	17.0	5.5
S. tenuicaudata			0.5		4.2	1.4		1.0	0.6		1.1	1.7			3.1			
S. sp. 1		1.9	0.5								1.1	1.7						0.7
S. sp. 2			0.5		1.2			0.5										
Metalinhomoeus additus	0.8	1.9								0.9				4.3	0.6	1.3		3.4
M. setosus	1.5	2.0	0.5					1.0	1.1				2.9	1.7	0.6	0.7		0.7
M. dimorphus			1.6	0.8				0.5		0.9	1.1	8.5	1.0			4.5		0.7

the word "habitat," as was pointed out by Bagenal (1951), should be used in its narrowest sense and be equivalent to 'microhabitat.' Even so, natural conditions are rarely homogeneous and populations living in a well-defined habitat will deviate to a greater or lesser degree from the type of species composition requiredy by Gause's principle. Much depends on whether by "same" one implies "identical" or "similar." Riley (1953) has summarized the methods by which species with superficially identical, but in reality not quite identical ecological requirements, manage to live in what looks like the same habitat but what in reality is a mosaic of functional niches.

Therefore, if we believe Gause's principle to be valid in theory, deviations from it in nature can be considered as reflecting the degree of homogeneity of the habitat from which the examined population was derived. This is an application of the principle which seems to have attracted little attention yet it might prove to be of interest, particularly with respect to the benthic meio- and microfauna. These small animals live in an environment where the degree of homogeneity cannot readily be ascertained. We do not know beforehand what effect small physiographic differences of the environment may have on the animals. Thus the most convenient way to establish the presence or absence of ecological niches within an otherwise well defined habitat may be by studying the species composition within that habitat. If the population, or any important taxonomic group, is strongly dominated at a given time by one species then the habitat can be considered fairly homogeneous with respect to that population or taxonomic group. If there are several species of about equal dominance the presence of different niches within the habitat is indicated.

In aquatic environments the pelagial can be expected to offer homogeneous conditions over fairly large stretches. This is suggested by an analysis of the limnetic zooplankton (Pennak 1957) which revealed a very high abundance of the dominant species within each of the three major groups: copepods, cladocerans and rotifers. From 27 Colorado lakes Pennak found that the dominant species constituted 92.9% in copepods, 84.7% in cladocerans, 63.6% in rotifers while there were correspondingly low values for the next most abundant species.

A very different picture emerges if the nematode fauna of marine benthic habitats is compared. Figure 1 indicates that at none of the three stations does the nematode fauna possess a degree of homogeneity similar to that of the limnetic zooplankton. At each station there occurs a great number of species and the per cent abundance of

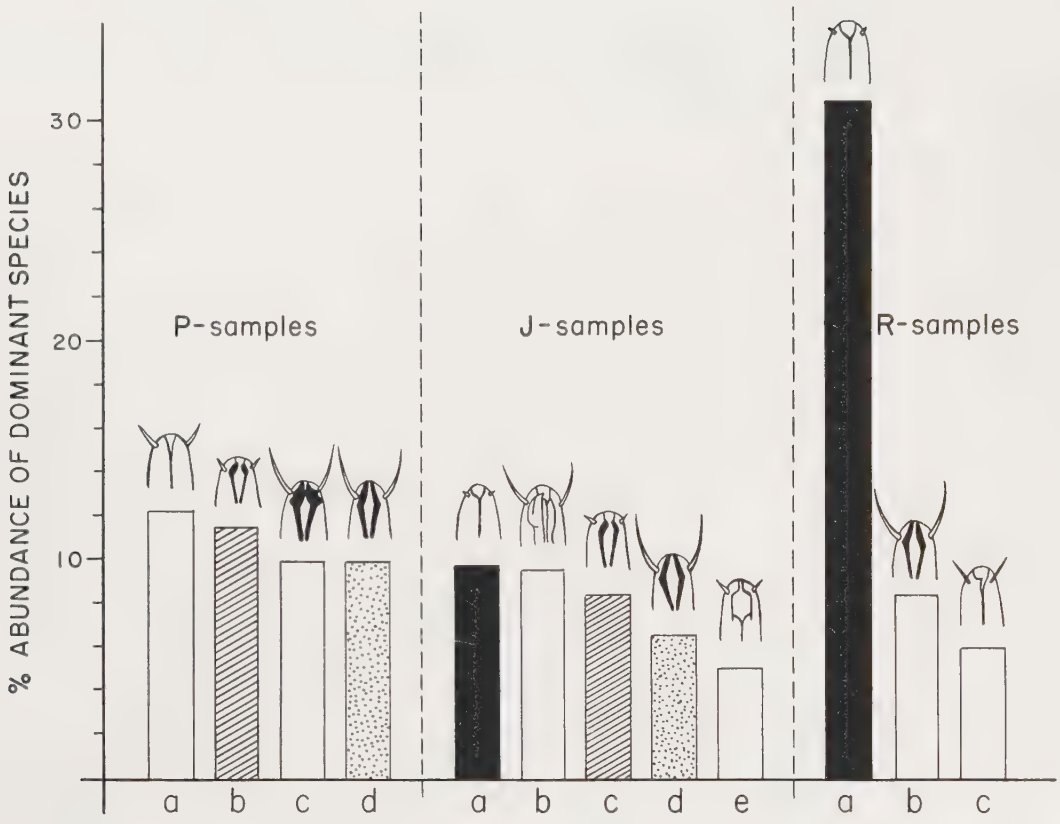

FIG. 4. The dominant nematode species at the three stations studied. The height of each column indicates the average abundance of each species at the respective station. Identical species are characterized by identical conventions. The species represented are the following:
P-samples: a: *Anticoma litoris*, b: *Dorylaimopsis metatypicus*, c: *Odontophora pugilator*, d: *O. papusi*.
J-samples: a: *Terschellingia longicaudata*, b: *Neochromadora pistillata*, c: *Dorylaimopsis metatypicus*, d: *Odontophora papusi*, e: *Filipjevinema potor*.
R-samples: a: *Terschellingia longicaudata*, b: *Odontophora löffleri*, c: *Sabatiera ornata*.

the dominant nematode does not approach that of the dominant copepod, cladoceran or rotifer in Pennak's investigation. However, there exist also significant differences between the three stations at Buzzards Bay. At the fine deposit station (R) the dominance of the most abundant species, *Terschellingia longicaudata,* is quite well pronounced, whereas at the sandy stations (J and P) there are three or four more or less equally dominant species. This indicates that, with respect to the nematode fauna, stations P and J represent a more heterogeneous habitat than station R. It might be speculated that in the sandy habitats the sand grains and the interstitial deposits represent two quite different sources of food, equivalent to two niches within the overall habitat. This is also suggested by the distribution of feeding types shown in Figure 4. Further splitting up of the habitats could be based on vertical layering of the substrate, accompanied by a segregation of the nematode fauna into vertically distinct components.

The existence of microhabitats within a more general habitat can also be inferred from the distribution of closely related species. Bagenal (1951) in clarifying the findings of Williams (1947) states "closely

related species are more likely to be found in *similar,* though not identical, habitats." Thus it might very well be that microhabitats within a more general habitat will often be occupied by closely related species, or, conversely, if closely related species are found within one well-defined habitat, the segregation of the habitat into microhabitats is indicated.

In order to test this assumption, Table 7 lists all genera which were represented by more than two moderately abundant species. Within the genus *Odontophora* the occurrence of closely related species at station P is particularly striking. *O. pugilator* and *O. papusi* do not seem to compete for the same sort of food since both were about equally abundant in several samples although each sample covered an area of only 10 cm^2. As might be inferred from Figure 4, there is a clear difference in the structure of the buccal plates of these two species. *O. pugilator* has much more powerful plates than *O. papusi,* which may reflect the adaptation to different sources of food. On the other hand, the only case of simultaneous occurrence of closely related but moderately abundant species at station R seems to show that the representatives of the genus *Sabatiera* compete with each other, since when S. *hilarula* is abundant (R–1), S. *ornata* is rare, and, conversely, when S. *ornata* is abundant (R–3, R–4), S. *hilarula* is rare. The occurrence of several species of *Sabatiera* in one sample is common for marine mud bottoms and has been discussed before (Wieser 1958a, b).

Thus the distribution of closely related nematode species at the three stations again points toward the heterogeneity of the habitat with the highest percentage of sand (station P). The case for the intermediate habitat (station J) is not conclusive in this example. It is of interest that the macrofauna shows a pattern of distribution similar to that of the meiofauna; station P is dominated by three closely related species of amphipods, *Ampelisca spinipes, A. macrocephala* and *Byblis serrata,* while at station R the dominant species are not at all closely related (Sanders 1958). This parallelism is the more remarkable since the amphipods of station P are filter feeders whereas the nematodes are substrate feeders.

Feeding habits

Most representatives of the meiofauna feed on the substrate itself, either on the epigrowth on sandgrains, or by ingesting the fine deposits. Turbellarians, members of the subfamily Halacarinae and a number of nematodes have been considered predators but it becomes increasingly clear that many of the marine benthic animals that have been called "predators" actually behave as deposits feeders most of the time. This was shown by Sanders (1956) for the polychaete *Nephthys incisa* and by Thorson (1957) for the brittle star *Amphiura.* In a previous paper Wieser (1953) conjectured that a large portion of the nematode fauna were predators because of their strong buccal armature and the occasional appearance of metazoan remains in their guts. Possibly most of these forms are deposit feeders; Perkins (1958) found the gut content of 16 specimens with strong buccal armature to consist chiefly of diatoms, bacteria and "what were possibly minute flagellates."

As far as the feeding habits of the meiofauna are concerned, the main distinction seems to be between "epistrate feeders" and "deposit feeders" as supposed by Remane (1933). Both these types probably include species of various degrees of food specifity but there is insufficient evidence to permit any further sub-grouping. The predominance of species which have been reported to live on diatoms (*cf.* Remane 1933, Perkins 1958) may be somewhat misleading since diatoms are the most easily recognized food component. However, there can be no doubt that both sessile and vagile diatoms constitute one of the major food sources in marine shallow water substrates.

The two coarse bottom stations (P,J) are characterized by the more or less equal abundance of four or five species comprising four types of buccal structure. At station P we find on the one hand *Anticoma litoris,* a species with a minute buccal

cavity, on the other hand *Dorylaimopsis metatypicus, Odonotophora papusi* and *O. pugilator,* three species equipped with fairly powerful buccal plates or mandibles. At station J we find two species with unarmed, cup-shaped or cylindrical buccal cavity, one species with relatively small buccal teeth and two of the more strongly armed species also occurring at station P. In contrast to this situation, the samples from the soft bottom station R are dominated by *Terschellingia longicaudata,* a species with unarmed, cup-shaped buccal cavity, and the third most abundant species is *Sabatiera ornata,* which has a buccal cavity of similar structure.

It may be assumed, therefore, that *Terschellingia longicaudata* and *Sabatiera ornata* with their buccal armature are "deposit feeders," while *Odontophora* spp. and *Dorylaimopsis metatypicus* are "epistrate feeders," scraping food off sand grains. However, it is not likely that every species of benthic animal can be assigned unequivocally to either of these two types, and as the so-called "predators" show, there exist also animals of more omnivorous habits. Similarly, some epistrate feeders may be able to feed on fine deposits and *vice versa.* A possible example of the first case is *Dorylaimopsis metatypicus* which occurred at all stations in relative abundance.

At station J the species without buccal armature (*Terschellingia* and *Filipjevinema*) are about as abundant as those with buccal armature (*Neochromadora, Dorylaimopsis* and *Odontophora*). This is in agreement with the intermediate position of station J on the silt-clay scale (Table 1).

Of the meiofauna groups less numerous than the nematodes, the kinorhynchs are pure deposit feeders. The ostracods have been considered as deposit feeders (Remane 1933, Mare 1942) while Perkins (1958) found the gut of many specimens of *Leptocythere pellucida* filled with diatoms. The harpacticoid copepods are either epistrate feeders or deposit feeders (Remane 1933). Perkins found in the guts of several species mainly diatoms, "vegetable matter of uncertain origin" and detritus. Turbellarians are generally regarded as predators but Webb (1956) observed rhabdocoeles feeding on diatoms and green flagellates in the laboratory.

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BENTHIC STUDIES IN BUZZARDS BAY
III. THE STRUCTURE OF THE SOFT-BOTTOM COMMUNITY[1]

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ABSTRACT

A series of 24 samples was taken at periodic intervals at a single locality in Buzzards Bay from February 1956 to January 1958. With the exception of 4 samples which departed markedly from the others in regard to sediment composition, very high indices of faunal affinity were obtained within the series. The silt-clay fraction of the sediment in the 20 samples with high faunal indices varied from 78–91%, and when the contained species were ranked by abundance, the commoner species achieved approximately the same rank from sample to sample. Thus, 8 or 9 species are a constant part of the biological environment of this association, and there is an approximately constant numerical proportionality among them. Seventy-nine species were obtained from the 20 samples of typical sediment composition. However, 11 species comprised almost 95% of the total fauna by number while the lamellibranch *Nucula proxima* (58.86%) and the polychaete *Nephthys incisa* (17.21%) were commonest. Ten species make up 95% of the total biomass. Thus the community, both numerically and by biomass, is characterized by pronounced dominance of few species. The niches of the 9 most common species, representing 93.5% of the community by number, were categorized by method of feeding, kind of food and spatial distribution. Considering only these few factors, it was possible to demonstrate certain differences in niche preference. The relationship of animal numbers to animal weight revealed the expected pyramid of numbers with very few organisms in the largest weight categories and numerous individuals in the smaller weight groups. However, when the biomass within each weight category was determined, the expected inverted pyramid did not result. Numbers are considered more valid than biomass in quantitative benthic studies, since only 0.15% of the fauna constitute 55.17% of the entire weight. The presence or absence of a rare, randomly distributed large animal may alter the biomass of an individual sample by two orders of magnitude.

INTRODUCTION

This paper, the third in a series dealing with the benthic fauna of Buzzards Bay, Massachusetts, is concerned primarily with the community of animals present in the finer sediments. The term "community" is used in this study to mean a group of species that show a high degree of association by tending to reoccur together.

I am indebted to Dr. Wolfgang Wieser for numerous discussions regarding this study and for making available to me some of his unpublished data concerning the meiofauna.

METHODS

From the initial survey (Sanders 1958), Buzzards Bay station R (41° 30′ N 70° 31′ W) was selected as being characteristic of the *Nephthys incisa-Nucula proxima* community, the fauna typically present in the softer sediments. While most of the sediment at this locality is composed largely of silts and clays, subsequent samplings did reveal patchiness. At approximately monthly intervals from February 1, 1956 to March 3, 1957, paired quantitative samples were taken at this station, which is situated in about 19 m of water, using a modification of the Forster anchor dredge. For the following 10-month period (April 1957 to January 1958) single samples were collected at appreciably longer intervals of time.

A small aliquot of the sediment from each sample was retained and analysed for particle-size composition. The sands were divided into various size categories using a graded series of sieves while the silts and clay fractions were determined by the pipetting method (Soil Survey Staff 1951). The results of the mechanical analyses are given in Table 1.

[1] Contribution No. 1033 from the Woods Hole Oceanographic Institution. This research was supported by National Science Foundation Grant G–4812.

TABLE 1. *The particle size analysis by per cent weight of the 24 samples from station R in Buzzards Bay*

Sample	Date	Gravel		Sand					Silt					Clay	
		(8.0–4.0 mm)	(3.9–2.0 mm)	(1.9–1.0 mm)	(0.9–0.5 mm)	(0.49–0.25 mm)	(0.24–0.125 mm)	(0.124–0.062 mm)	(61–31μ)	(30–16μ)	(15.8 μ)	(7–4 μ)	(3–2 μ)	(<2μ)	0/0< 50μ
1RA	2/1/56		0.6	0.2	0.1	0.3	1.4	3.3	24.4	21.1	10.1	12.0	8.1	18.4	85.8
1RB	2/1/56		0.6	0.4	0.8	1.3	2.1	3.2	26.7	16.0	13.4	11.4	7.4	16.7	82.5
2RA	3/13/56			0.1	0.5	2.0	3.2	3.8	34.9	25.4	5.3	7.4	0.4	17.0	78.5
2RB	3/13/56			0.1	0.5	1.4	1.7	3.3	29.3	17.6	11.7	11.7	11.7	11.0	83.0
3RA	4/27/56			0.2	1.3	3.4	5.3	4.6	23.7	12.5	13.8	8.1	10.6	6.5	67.1
4RA	6/6/56				0.6	1.5	1.6	2.6	24.7	15.9	14.8	13.2	5.4	19.7	85.3
4RB	6/6/56		1.2	1.4	5.7	13.6	10.1	3.8	18.5	12.1	7.8	6.3	7.8	11.7	57.9
6RA	7/12/56	1.8	5.5	5.7	15.8	26.2	15.7	0.4	8.9	3.9	3.6	3.9	3.3	5.3	25.9
6RB	7/12/56				0.1	0.4	1.1	1.8	18.4	15.4	7.7	19.9	14.1	21.1	90.3
7RA	8/14/56			0.1	0.1	0.3	1.0	2.9	32.1	17.5	12.7	12.2	11.6	9.5	84.7
7RB	8/14/56			0.1	0.2	0.5	0.8	2.2	28.0	15.9	23.3	10.1	9.0	9.9	86.7
8RA	9/6/56			0.1	0.3	0.5	1.2	2.7	31.8	14.7	13.9	13.1	7.3	14.4	84.4
8RB	9/6/56		0.6	0.2	0.4	1.0	3.4	3.8	29.1	16.4	12.9	10.7	7.6	13.9	80.7
9RA	10/4/56		0.2	0.9	5.4	16.8	16.1	6.4	15.1	8.7	7.4	4.8	5.2	13.0	49.1
9RB	10/4/56		0.2	1.3	0.4	3.8	4.1	4.0	20.1	15.9	11.8	9.4	8.1	20.9	79.4
10RA	11/5/56			0.2	0.3	0.4	1.0	2.2	23.6	16.4	14.6	15.5	4.6	21.2	87.9
10RB	11/5/56			0.2	0.2	0.5	1.1	2.3	25.8	16.5	15.5	12.7	9.6	15.6	86.9
11RA	12/19/56		1.3	0.2	0.1	0.2	1.3	4.7	29.6	10.6	17.3	11.8	8.4	14.5	82.1
11RB	12/19/56			0.1	0.1	0.2	1.7	5.5	17.5	17.1	14.5	12.8	9.8	20.7	86.5
12RA	3/6/57			0.1	0.2	0.5	1.2	2.2	26.9	17.4	12.8	13.1	7.1	18.5	86.7
12RB	3/6/57		0.3	0.1	0.1	0.4	1.1	2.7	21.5	19.4	4.5	21.8	8.3	19.8	88.0
14R	6/20/57	0.1	0.2	0.4	1.0	2.2	3.7	5.3	25.4	14.9	12.7	9.7	0.2	24.2	78.4
15R	9/12/57			0.1	0.1	0.6	1.7	3.5	27.2	17.9	11.6	7.6	9.6	20.1	84.8
17R	1/30/58		0.3	0.2	0.4	1.2	1.8	3.0	25.0	14.7	12.2	11.0	7.9	22.3	84.6

The volume of the remainder of the sample was measured and the contents were passed through a screen with 0.2 mm mesh openings. The writer has demonstrated in previous studies using a series of graded screens, that very large fractions of the smaller sized species and most of the younger stages of the larger forms are not retained by the larger meshed screens. Obviously the loss of such faunal components would seriously compromise the validity of the results, and the use of a very fine seive is essential to this study.

The sediment

The predominant sediment components at this station are the silts and clays (see Table 1). Hereafter the term "% silt-clay" is used to mean the part of the sediment that is less than 50μ. This fraction is listed in the column at the extreme right in Table 1. Such a procedure was adopted in order to make the present investigation comparable with earlier studies (Sanders 1956, 1958). In most cases this silt-clay fraction makes up from 78 to 91% of the samples. If an undisturbed core is taken, the sediment can be clearly divided into two parts; a lower consolidated gray silty zone and a brown unconsolidated flocculent layer which comprises the top two or three centimeters of the substratum. The upper layer, as observed from core samples, is readily moved even by the slightest disturbance. Apparently this flocculent layer sloshes continuously back and forth over the consolidated sediment. The layer is appreciably thicker in such an environment than on coarser sediments and its accumulation here is most probably the result of the much reduced bottom currents characteristic of areas of deposition.

It is reasonable to suppose that the organic content of the flocculent layer should be appreciably higher than that of the underlying sediment since the "rain" of detritus from the water column as well as broken fragments of seaweed are being incorporated continuously into it. When samples from the two zones were placed in an oven at 500°C for 24 hours, 7.4% of the flocculent sample was burned as compared

TABLE 2. *Showing the actual number of various species in each of the R station samples*

Species	1RA	1RB	2RA	2RB	3RA	3RB	4RA	4RB	6RA	6RB	7RA	7RB	8RA	8RB	9RA	9RB	10RA	10RB	11RA	11RB	12RA	12RB	14R	15R	17R
Polychaeta:																									
Nephthys incisa	143	53	13	45	13	77	36	17	9	325	171	550	223	23	64	45	187	154	19	105	242	129	129	36	61
Ninoe nigripes	17	8	11	25	5	77	12	32	60	22	23	94	70	5	108	12	84	47	2	19	76	60	34	13	37
Lumbrinereis tenuis	93	24	2	25	3	15	2	10	15	15	16	32	8	—	4	3	10	18	2	10	11	5	2	4	8
Lumbrinereis fragilis						4		1														1			2
Arabella iricolor		1				5	1	2	5	1			2		1	1	1	2		1	4	3		1	1
Drilonereis longa		1		1		6			1												1	1			
Diopatra cuprea						1			2			2			3						1				
Harmothoe extenuata										1															
Pholoe minuta	1					6		1							3	3									
Syllis cornuta		1				7		1					1		2			1							
Phyllodoce arenae																									1
Paranaitis speciosa								1																	
Nereis grayei									1															1	
Glycera americana						4		1	1				1				2				5	17		1	2
Dorvillea caeca	57				22	14				1		1	9				3	4		14					
Scolopos acuta						1																			
Scalibregma inflatum						6															2		1		
Aricidea jeffreysii	12	4	4	5		36		2					1		2		1	1			10	2		2	1
Paraonis gracilis						1	1	1		1	1	4	1	2		2	2	4	1	1	1		1		1
Tharyx sp.	57		4	15	1	14	1	2	2		1	2			1	3	2			3	2	1	1	2	34
? *Spio filicornis*	63	1	4	5	1	7	1			2		2	5			2	7			3	1		1	3	
Capitellid	14	2	1			4			1	2						1	2					2		2	2
Spiochaetopterus oculatus																				1	1	2	2	1	1
Flabelligera affinis								1	4	1					1					1					1
Maldanopsis elongata	1		1							1	1		2	1	4	3	4	1			3	3			1
Praxillella praetermissa					1																				
Melinna cristata	2	4	1	1		1	1			1		1	1	1	3		3	2							
Ampharete arctica						4		1		20		2			1										1
? *Nicolea* sp.					1																				
Asabellides oculata																						1			
Polycirrus sp.				2		10				1															
Pectinaria gouldii	5	1		2		1		1				1			1		1	1							
Exogone sp.									1			1													
Oligochaeta:						1											2				1			5	

Turbellaria:																									
Anaperus sp.																					2				5
Flatworm b.															1			1							1
Nemertinea:																									
Tubolonus pellucidus		2	1	2		1	2									1				1				2	8
Micrura leidyi	6	1					1				1													1	1
Sipunculoidea:																									
Phascolon strombi				5				1														1			
Phascolosoma verrilli	1				1				4	1															
Enteropneusta:																									
Dolichoglossus Kowalevskii	1	3	2		1	2																			1
Tunicata:																									
Bostrichobranchus pilularis				5		6										1	3	2	2	6	3	1	14		
Anthozoa:																									
Cerianthus americana	4	1							1							2						1		1	1
Edwardsia sp.								1				1	1			1						1		1	1
Mollusca:																									
Nucula proxima	1940	1180	82	422	9	274	116	1	3	256	241	1170	743	40	3	184	504	290	8	105	560	280	592	551	295
Nucula delphinodonta	4	4		1			1	1	1	10		9	1		2		2					2	1	1	1
Yoldia limatula		17	1	5		2	1			4	1	6		1				1					1	1	
Macoma tenta		8	1	3		2		1		1						1	1	2					2		2
Callocardia morrhuana	73	49	3	43	4	19	5	21	2	31	29	128	8	2	1	3	18	12	2	10	36	19	22	1	11
Mulinia lateralis	3	2		3		1										1			1						
Astarte subaequilatera	2										1	3						1				1	1		1
Astarte undata								2								1									
Arca pextata	2					1						2					1				1				
Cerastoderma pinnulatum	1		1																		1	1			
Pandora gouldiana																					1				1
Commensal clam								5															3		
Cylichna orzya	138	117	17	63	2	36	2			29	14	35	5		1	5	28	29	1	2	38	25	13	16	71
Retusa caniculata	17	11	4	13		5	2			12	2	11	1		1	1	6	10	1	1	10	9	4	1	4
Acteon punctostriatus	3	2		3		1									1			1							
Turbonilla a	13	34	1	10	1	11	3	4		3		2	4			8	17	12	1	7	7	8	6	4	5
Turbonilla b	1								4						26						1	1			
Crepidula plana	1		1																		1	1			
Anachis avara															1										

TABLE 2. *Continued*

Species	1RA	1RB	2RA	2RB	3RA	3RB	4RA	4RB	6RA	6RB	7RA	7RB	8RA	8RB	9RA	9RB	10RA	10RB	11RA	11RB	12RA	12RB	14R	15R	17R
Mitrella lunata		1								3					3										1
Nassarius triviattatus	1	3		7					4	2	5	11	3	1	3		1			1		2	3	5	
Eupleura caudata			1	2				1		1							1					1		1	
Bela turricola	2	2		1								1					1					1			
Natica pusilla				1				1										3							
Polynices triseriata		1		1		1							1								1				
Gastropod a												1													
Crustacea:																									
Hutchinsoniella macracantha	2			2	23	3	———		75	———		15	1	—68—		— 25 —		— 58 —		1	28	— 68 —			10	2
Ampelisca spinipes	3	5		1		168	1	17	2			2	9			32	4	13	10	1	2			1	1	1
Ampelisca macrocephala						36											1				1					
Byblis serrata						9		2																	
Leptocheirus pinguis								34	84						3						1		4		
Unciola irrorata	18	1			9			7	1						17	2		1		2	15	1	1		17
Corophium acherusicum	1								1			1				1	1		1		1	2		1	
Corophium insidiosum									1										1						
Corophium tuberculatum															2										
Siphonoecetes smithianus						1																			
Lysianopsis alba	1																								
Stenothoe cypris	1																								
Batea secunda					2													1							
Hyperia galba	1																								
Aeginella longicornis									1																1
Amphipod A								2	1								1								
Edotea triloba	1							1			1	1				1	7	2		3	1	4	2		14
Oxyurostylis smithi	1	2		1		1						1											1	3	
Diastylis sp.	1	1		1		1										1		1					2	1	
Eudorella emarginata	1																								
Petalosarsia declivus	1																								
Pagurus annulipes									1			1													
Libinia sp.	1																								
Pinnixia cylindrica									1															1	
Pycnogonida:																									
Anoplodactylus lentus												1									1				1
Ophiuroidea:																				1					

to 6.0% for the consolidated sediment sample. It would seem then that the amount of organic matter present in the two layers is not appreciably different and therefore the food resources for the deposit-feeders are approximately as abundant in one zone as in the other.

However, there may be a qualitative difference in the organic matter of the two zones. Some very preliminary measurements of free small chain sugars in the sediment seem highly suggestive. Detectable quantities of these substances were found only in the uppermost two centimeters. Such sugars should serve as a ready food source for the deposit-feeders. The organic matter in the consolidated sediments, being separated from the sources of detritus both in time and space, may be refractory or "fossil" in nature and thus less utilizable as a food source.

The distribution of the animals in the sediment column further supports such a conjecture, although anaerobic conditions deeper in the sediment may largely determine the pattern. A series of cores was split approximately at the interface between the two sediment zones. It should be emphasized that there was considerable contamination of one zone by the other. Yet nearly 75% of the animals were present in the upper zone and the remaining animals were limited to the top 2 cm of the consolidated layer. In another series of cores, none of the approximately one hundred specimens were found below a depth of 6 cm.

Faunal homogeneity

The numerical distribution of the fauna in the 24 samples comprising this series is shown in Table 2.

It is obviously necessary in a community study to demonstrate that the species components of the included samples show faunal similarity. To measure such affinities a matrix method, the "trellis diagram," was adopted. The percentage composition of the various species in each sample is determined. The samples are then arranged linearly at right angles along the ordinate and abcissa and all possible pairs are compared regarding their faunal content. The resultant value, the "index of affinity," is a measure of the percentage of the fauna common to a pair of samples and it is obtained by summing the smaller percentages of those species present in both samples. The table is then rearranged so that the samples with the highest values are brought into closer proximity. In this way the samples that are most ecologically alike are grouped together. The resulting diagram is shown in Figure 1.

It is immediately evident from this figure that samples 9RA, 6RA, 4RB and 3RA have low indices of affinity; that is, these 4 samples have a markedly different faunal composition from the other 20. Inspection of Table 1 suggests a possible reason for this difference. These same 4 samples agree in having much lower percentages of silt-clay. Whereas the sediments of the 20 samples with high indices of affinity range from 78.4 to 90.3% silt-clay, with a mean of 84.3%, the silt-clay percentages of the 4 samples in question are as follows: 3RA, 67.1; 4RB, 57.9; 9RA, 49.1; 6RA, 25.9. Another sample, 3RB, was omitted from consideration when it became evident that a part of sample 3PB from the sand bottom community series was accidentally included with it.

An average index of affinity value for all possible sample pairs (276) is 56.6. If the four aberrant samples are excluded, the value of the remaining paired combinations (190) becomes 69.3. In order to determine the significance of this number, a comparison with other values, either given in the literature or calculated from other studies, is summarized in Table 3.

From Wieser's (1960) investigation of the meiofauna of Buzzards Bay, the average correlation coefficient is given for all samples and for the four samples collected at station R with a homogenous sediment composition. Correlation values were calculated for the macrofaunal survey of Buzzards Bay (Sanders 1958) and indices are given for all stations included in the survey, those stations carrying a fauna largely characteristic of the *Ampelisca* spp. com-

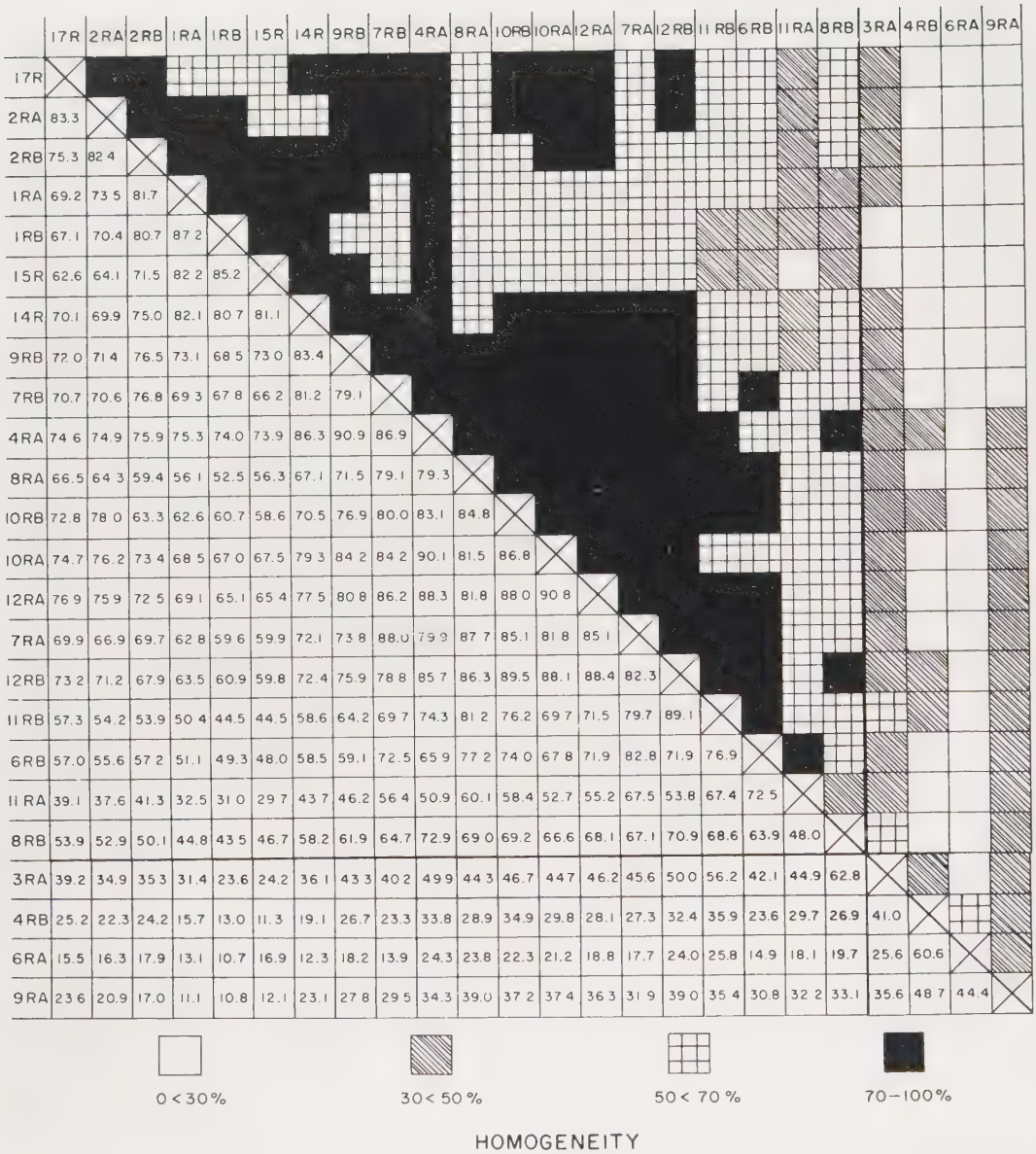

FIG. 1. A comparison of the average faunal index of affinity at station R with indices from other studies.

munity, and the stations predominantly with faunal elements present in the *Nephthys incisa-Nucula proxima* community. Renkonnen (1944) used the trellis diagram for a study of beetles inhabiting the supralittoral zone of a lake in southwest Finland. From his analysis he recognized 5 communities; the average correlation values within each of his communities are also given in Table 3. Finally Macfadyen (1954) used the same technique, together with other methods of analysis, in his investigation of the invertebrate fauna of Jan Mayen Island (East Greenland). Measuring the affinites among the Collembola species, he found two associations and the average correlation value within each association is included.

Table 3 reveals that the present study gives by far the highest index of affinity. This value was obtained despite the fact

TABLE 3. *A comparison of the average faunal index of affinity at station R with indices from other studies*

	Index of Affinity
Macrofauna at station R (all samples)	56.6
Macrofauna at station R less 5 samples of aberrant sediment composition	69.3
Meiofauna of Buzzards Bay (Wieser 1960)	27.2
Meiofauna of R samples with similar sediment composition (*op. cit.*)	55.7
Macrofauna of Buzzards Bay (Sanders 1958)	21.4
Ampelisca spp. community (Sanders 1958)	31.2
Nephthys incisa–Nucula proxima community (Sanders 1958)	37.2
Beetle fauna from lake shore in SW Finland (Renkonnen 1944)	
Total of 40 stations	24.3
Community 1 (1 station)	—
Community 2 (4 stations)	54.2
Community 3 (23 stations)	33.5
Community 4 (15 stations)	34.2
Community 5 (16 stations)	36.9
Collembola of Jan Mayen Island (Macfadyen 1954)	
Association 1 (11 species)	24.7
Association 2 (9 species)	24.6

that, in contrast to the other studies, the samples were taken at all seasons of the year. Because recruitment is not synchronous in the dominant species, the numerical proportionality should be constantly altering and one should expect a lowered index of affinity. Therefore, it seems valid to conclude that the fauna at station R represents a very stable and homogenous assemblage except in the aberrant sediments. However, it should be mentioned that station R was selected because it was thought to be faunally homogeneous.

There are certain weaknesses inherent in this method of analysis. No discrimination is made against ubiquitous species (see Macfayden 1954). Furthermore, the method is not quantitative and unless care is taken gross errors may be introduced. For example, species A at a station X carrying a sparse fauna may comprise 80% of the population while at another station, Y, with a more numerous fauna the same species may constitute only 2% of the population. It is conceivable, however, that species A may be numerically more common at Station Y. Yet by the method of analysis used, species A is the dominant species at station X and it will be assumed that the environmental conditions will be more favorable at a station (X) where the species is dominant than at a station where it is not (Y).

Neither of these criticisms seem particularly pertinent to the present study, however. In Buzzards Bay there appears to be no species that is both ubiquitous and very common (see Tables 3 and 4, Sanders 1958). Concerning the second point, if the samples with aberrant sediments are omitted (3RA, 4RB, 6RA and 9 RA), all the remaining samples are of a single sediment type.

The community

Since the association of animals appears to possess the features of a community as the term was defined earlier in this paper, it would be of interest to attempt to determine the species structure of such a natural assemblage.

The data presented in Table 4 show the evidence of dominance by a few species. In fact, the two most common forms, the lamellibranch *Nucula proxima* and the polychaete *Nephthys incisa* make up respectively about 59% and 17% by number of the community. Together the two species comprise more than 76% of the fauna. Ninety-five per cent of the assemblage is formed by only 11 of the 79 species present. If the community is evaluated on the basis of biomass rather than number the same pronounced dominance by a few species is evident. Only 13 species make up 95% of the biomass. The per cent composition by weight of these species are shown in Table 4. Only some of the numerically more abundant species contribute significantly to the biomass (*Nephthys, Nucula, Callocardia* and *Ninoe*) while certain numerically rare forms such as the tunicate *Bostrichobranchus pilularis,* the nemertean *Micrura leidyi,* and the polychaetes *Arabella iricolor* and *Lumbrinereis fragilis,* because of their large individual size, represent major biomass components of the fauna.

Such a pattern could result from the bias of a few unusually large samples. To test such a possibility, each sample was ranked

TABLE 4. *The structure of the* Nephthys incisa–Nucula proxima *community at station R. The species present in the 20 samples characterized by "typical" sediment composition (78–91% silt-clay) are listed according to their numerical abundance. The totals given (column 2) are the sum of the numbers of individuals of the given species in the 20 samples. Columns 3, 4, 5, 6 and 7 list respectively the cumulative per cent by number, the per cent composition by number, the dry weights, the per cent composition by weight and feeding type.*

Rank by no.	Species	No.	Cumulative % by no.	% of fauna by no.	Dry wt. (g.)	% by wt.	Rank by wt.	Feeding Type[1]
1	*Nucula proxima*	9195	58.86	58.86	2.9694	13.98	4	SDF
2	*Nephthys incisa*	2689	76.07	17.21	6.1489	28.95	1	NSDF
3	*Ninoe nigripes*	671	80.37	4.30	0.3791	1.78	8	NSDF
4	*Cylichna orzya*	647	84.51	4.14	0.0782			?
5	*Callocardia morrhuana*	525	87.87	3.36	3.1803	14.97	3	SF
6	*Hutchinsoniella macracantha*	307	89.84	1.97	0.0583			NSDF
7	*Lumbrinereis tenuis*	286	91.67	1.83	0.0620			NSDF
8	*Turbonilla* a	145	92.60	0.93	0.0053			?
9	?*Spio filicornis*	135	93.46	0.86	0.0186			SDF
10	*Retusa caniculata*	120	94.23	0.77	0.0440			?C
11	*Dorvillea caeca*	103	94.89	0.66	0.0099			?C
12	*Tharyx* sp.	89	95.46	0.57	0.0100			SDF
13	*Unciola irrorata*	58	95.83	0.37	0.0286			SDF
14	*Ampelisca spinipes*	54	96.18	0.35	0.0324			SF
15	*Nassarius triviattatus*	45	96.47	0.29	0.1726	0.81	9	NSDF
16	*Bostrichobranchus pilularis*	40	96.73	0.26	4.9878	23.49	2	SF
17	*Yoldia limatula*	39	96.98	0.25	0.1084	0.51	13	SDF
18	*Nucula delphinodonta*	37	97.22	0.24	0.0060			SDF
19	*Edotea triloba*	37	97.46	0.24	0.0381			S
20	*Paraonis gracilis*	31	97.66	0.20	0.0032			SDF
21	*Melinna cristata*	25	97.82	0.16	0.0461			SDF
22	Capitellid	24	97.97	0.15	0.0007			NSDF
23	*Ampharete arctica*	24	98.12	0.15	0.0154			SDF
24	*Macoma tenta*	22	98.26	0.14	0.0094			SDF
25	*Arabella iricolor*	19	98.36	0.12	0.8000	3.77	6	?C
26	*Tubolonus pellucidus*	19	98.50	0.12	0.0019			?C
27	*Maldanopsis elongata*	17	98.61	0.11	0.0488			NSDF
28	*Mulinia lateralis*	12	98.69	0.08	0.0059			SF
29	*Pectinaria gouldii*	11	98.76	0.07	0.0185			NSDF
30	*Micrura leidyi*	11	98.83	0.07	1.0263	4.83	5	C
31	*Oxyurostylis smithi*	9	98.89	0.06	0.0071			
32	*Cerianthus americana*	9	98.95	0.06	0.1578	0.74	10	
33	*Corophium acherusicum*	9	99.01	0.06	0.0049			
34	*Diastylis* sp.	8	99.06	0.05	0.0063			
35	*Acteon punctostriatus*	8	99.11	0.05	0.0004			
36	*Dolichoglossus kowalevskii*	8	99.16	0.05	0.0124			
37	*Spiochaetopterus oculatus*	8	99.21	0.05	0.0063			
38	*Bela turricola*	8	99.26	0.05	0.0053			
39	*Astarte subaequilatera*	8	99.31	0.05	0.0029			
40	*Eupleura caudata*	7	99.35	0.04	0.0069			
41	*Leptocheirus pinguis*	6	99.39	0.04	0.0213			
42	*Phascolon strombi*	6	99.43	0.04	0.0352			
43	*Anaperus* sp.	6	99.47	0.04	0.0004			
44	Oligochaeta	6	99.51	0.04	0.0002			
45	*Arca pextata*	6	99.55	0.04	0.0027			
46	*Mitrella lunata*	5	99.58	0.03	0.0033			
47	*Edwardsia* sp.	5	99.61	0.03	0.0500			
48	*Diopatra cuprea*	4	99.64	0.03	0.0468			
49	*Flabelligera affinis*	4	99.67	0.03	0.1403	0.66	11	
50	*Natica pusilla*	4	99.70	0.03	0.0017			
51	*Cerastoderma pinnulatum*	4	99.73	0.03	0.1382	0.65	12	
52	*Lumbrinereis fragilis*	3	99.75	0.02	0.3954	1.86	7	NSDF
53	*Glycera americana*	3	99.77	0.02	0.0480			
54	*Pholoe minuta*	3	99.79	0.02	0.0012			

TABLE 4. *Continued*

Rank by no.	Species	No.	Cumulative % by no.	% of fauna by no.	Dry wt. (g.)	% by wt.	Rank by wt.	Feeding type[1]
55	Flatworm b	3	99.81	0.02	0.0008			
56	*Anoplodactylus lentus*	3	99.83	0.02	0.0008			
57	*Polynices triseriata*	3	99.85	0.02	0.0047			
58	*Syllis cornuta*	2	99.86	0.01	0.0009			
59	*Polycirrus* sp.	2	99.87	0.01	0.0033			
60	*Phascolosoma verrilli*	2	99.88	0.01	0.0007			
61	*Ampelisca macrocephala*	2	99.89	0.01	0.0160			
62	*Turbonilla* b	2	99.90	0.01	0.0001			
63	*Pandora gouldiana*	2	99.91	0.01	0.0062			
64	*Crepidula plana*	2	99.92	0.01	0.0021			
65	*Batea secunda*	1						
66	*Astarte undata*	1	99.93	0.01				
67	*Nereis grayei*	1						
68	*Harmothoe extenuata*	1	99.94	0.01				
69	*Phyllodoce arenae*	1						
70	?*Nicolea* sp.	1	99.95	0.01				
71	*Asabellides oculata*	1						
72	*Corophium insidiosum*	1	99.96	0.01				
73	*Eudorella emarginata*	1			0.0150			
74	*Petalosarsia emarginata*	1	99.97	0.01				
75	*Pagurus annulipes*	1						
76	*Libinia* sp.	1	99.98	0.01				
77	*Pinnixia cylindrica*	1						
78	Ophiuroid	1	99.99	0.01				
79	Gastropod a	1						
	Total	15,622			21.2374			
	Number/m^2	8,985						
	Biomass/m^2				12.1858			

[1] SDF = Selective deposit-feeder
NSDF = Non-selective deposit-feeder
SF = Suspension-feeder
C = Carnivore
S = Scavenger

separately (Fager 1957), thus giving equal weight to each of the samples. Table 5 lists the frequency of a given species appearing as one of the 10 most abundant species (maximum frequency = 20); and the quantitative importance of the species. This latter factor is determined by ranking the species from 1 to 10 by abundance within each sample. A rank of 1 is given a value of 10 points; a rank of 2 equals 9 points; 3 is equivalent to 8 points,....., and a rank of 10 equals one point. Thus if a species is ranked first in all 20 samples, it will have 200 points, the highest possible score.

The results in Table 5 verify the findings given in Table 4. *Nucula proxima,* with almost the maximum possible points, is the most abundant species in 18 samples and is second most common in the remaining two giving a score of 198. *Nephthys incisa,* ranking first in two, second in 13 and third in 5 samples has the very high score of 177. Other species with high scores are the polychaete, *Ninoe nigripes* (132); the gastropod, *Cylichna orzya* (177); the lamellibranch, *Callocardia morrhuana* (109); the crustacean, *Hutchinsoniella macracantha* (83); and the polychaete, *Lumbrinereis tenuis* (62). Each of the above species is present in at least 80% and is one of the 10 most common species in 65–100% of the samples. Two other gastropods, *Turbonilla* a and *Retusa caniculata,* with somewhat lower scores (38 and 30) are present in 18 and 19 of the samples respectively. The analysis demonstrates, therefore, that these 9 species represent a very significant and constant part of the biological environment of this community. It follows that some knowledge of the niches of these species

TABLE 5. *Faunal frequency evaluation of the 20 samples with homogeneous sediment composition*

Species	1	2	3	4	5	6	7	8	9	10	Frequency	Frequency as one of ten most common species	Biological index value
Nucula proxima	18	2									20	20	198
Nephthys incisa	2	13	5								20	20	177
Ninoe nigripes			6	9	3				1	1	20	20	132
Cylichna orzya		4	2	4	2	2	3	1			19	18	117
Callocardia morrhuana			4	3	4	4	1	2	1		20	19	109
Hutchinsoniella macracantha		1	3	2	4	1	1	1			17	13	83
Lumbrinereis tenuis				1	1	5	2	3	3	1	19	16	62
Turbonilla a				1	1	1	2	2	2	2	18	11	38
Retusa caniculata							1	6	3	2	19	12	30
?*Spio filicornis*					1	2			1	2	16	6	20
Dorvillea capeca					2		2				11	4	20
Nassarius triviattatus						1	1	2		2	13	6	17
Ampelisca spinipes							1	1	4		14	6	15
Bostrichobranchus pilularis					1	1			1		10	3	13
Paraonis gracilis					1	1				1	15	3	12
Tharyx sp.							2	1		1	12	4	12
Unciola irrorata						1	1		1		9	3	11
Yoldia limatula							1	1		1	11	3	8
Edotea triloba							1			1	11	2	5
Ampharete arctica						1					2	1	5

would help in understanding the community structure.

The *Nephthys incisa-Nucula proxima* community can be considered to belong to the category defined by Elton (1946) as "animal communities in which species live on comparatively few basic sources of food." Besides aquatic benthic deposit-and suspension-feeders, he includes log-dwelling herbivores, soil animals, zooplankton, drift-line animals and blood-sucking ectoparasites in this category. In the *Nephthys incisa-Nucula proxima* community a minimum of 87.5% of the animals by number are deposit-feeders, obtaining their food from detritus either on or in the sediment. The other primary feeding type, the suspension-feeder, is present in much smaller numbers (4.3%) as might be expected from the nature of the sediment (see Sanders 1958).

Nucula proxima, the overwhelming dominant member of the community, normally lies just below the surface of the sediment feeding on the sediment immediately beneath it by long appendages derived from the palp. The inner surfaces of these structures are grooved and lined with ciliated epithelium (Drew 1899; Yonge 1939). Only the fine particles are moved along the groove to the palps where they are passed again by cilia to the mouth. *Nucula* then is a selective deposit-feeder.

The genus to which the other very abundant species, *Nephthys incisa*, belongs is considered to be carnivorous (Blegvad 1914; Smith 1932; Mare 1942; Holme 1949; Savilov 1957; Longhurst 1958). Yet in an earlier study in Long Island Sound (Sanders 1956) the writer has shown that the gut contents of those individuals examined were filled with sediments and there was no evidence of animal remains, indicating that the animal was primarily a deposit-feeder. Turpaeva (1957) also regards members of this genus as deposit-feeders.

These conclusions were further verified in the present study. Generally the gut contents were of two sorts. They either consisted of fine silt particles indicating the animal was ingesting the sediment from the lower gray consolidated zone or of large detrital particles, a few sand grains, intact diatoms including such benthic forms as *Gyrosigma* and various naviculoids as well as empty diatom frustules of both pelagic and benthic forms. Apparenly this actively burrowing form swallows the medium through which it moves indiscriminately ingesting sediment from both zones of the habitat. This does not imply that *Nephthys*

incisa cannot and would not act as a carnivore under certain circumstances. However in the community under discussion it represents such a significant fraction of the fauna both in regard to number and biomass (see Table 4) that it would not be feasible for the animal to be primarily predaceous and, indeed, the contents of the gut would certainly not support any such idea.

Third in abundance in this association is another polychaete, *Ninoe nigripes*, belonging to the family Lumbrinereidae. Being an errant polychaete with well developed jaws, and because other lumbrinereids are considered to be predators, this form too should be carnivorous. However, as in the case of *Nephthys*, stomach analysis revealed that the species is a non-selective deposit-feeder but unlike *Nephthys* the gray silty sediments were absent from the gut. The evidence therefore indicates that *Ninoe* feeds almost exclusively from the brown flocculent zone since the gut contents usually reveal large pieces of detritus, diatom frustules, benthic diatoms and few sand grains. Furthermore, *Ninoe* differs from *Nephthys* in being sedentary. It constructs a simple slime tube and the slow movement of the flocculent layer replenishes the source of its food.

The minute opistobranch gastropod, *Cylichna orzya*, is numerically the fourth most common species. In contrast to the previously mentioned forms, this animal is found only at the surface of the sediment. Because of its small size, the gut contents could not be satisfactorily analyzed.

The lamellibranch, *Callocardia morrhuana*, fifth in rank by number and third in rank by weight, is a representative of the other major primary consumer group, the suspension-feeders. It draws in its food by means of the inhalant siphon from the suspended matter in the overlying water column.

The sixth ranking species, surprisingly, is the remarkably primitive and supposedly very rare crustacean, *Hutchinsoniella macracantha*. The limb movements of this animal are metachronal and, as the space between two consecutive appendages enlarge, a suction chamber is formed from the interlimb space. The deposited material that is temporarily stirred up by the action of the large terminal spines on the inner ramus of the limb is sucked into this space. Subsequently, this material is squeezed into the mid-ventral food groove, where it is passed forward by spine-like processes at the base of the thoracic and maxillary limbs. The material in the food groove, gut, and in the fecal pellets was shown to be composed of detritus, diatom frustules, and sand grains. It is therefore a non-selective deposit-feeder eating in the flocculent non-consolidated sediment. A detailed study of the functional morphology of *Hutchinsoniella* is at present being undertaken by the writer.

The 6 species just discussed represent almost 90% of the entire macrofaunal assemblage. As they differ in spatial distribution, in their diet and methods of obtaining it, the niches of these animals are clearly different.

Another polychaete, *Lumbrinereis tenuis*, is ranked seventh in abundance in this community. Members of the genus *Lumbrinereis* (=*Lumbriconereis*) are classified as carnivores (Smith 1932, Savilov 1957, Longhurst 1958). The few gut contents of the species examined contained detritus. Like *Ninoe* the animal is sedentary and ensheathes itself in a slime tube. Furthermore, it feeds in the same manner and on the same sort of food as *Ninoe*. The few factors evaluated show no difference in the niches of these two lumbrinereid polychaetes.

The small pyramidellid gastropod designated as *Turbonilla* a, the eighth most common species, presents an enigma. All pyramidellids are ectoparasites (Fretter and Graham 1949); each species has a specific host, a sessile organism that protrudes part of its body to feed. All known hosts are either polychaetes and coelenterates that feed by tentacles or molluscs which are with a single exception epifaunal. In the former cases the pyramidellid pierces the tentacles or body wall with a stylet at the tip of a long eversible proboscis and sucks in the blood or body fluids; in the

latter situation it is the mantle that is pierced. There is, however, one report where the siphon of a lamellibranch was parasitized (Medcof 1948). As indicated in an earlier paper (Sanders 1958) it is difficult to accept this specific pyramidellid as being an ectoparasite since in slightly coarser sediments (50–70% silt-clay) it may comprise 25–50% of the fauna. Furthermore, there seem to be no suitable hosts among the species living in the same habitat, when abundance, size and mode of life are considered. The lamellibranch *Callocardia* might provide a possible exception; however the great majority of these clams are of the same small size as their possible parasite, a highly unlikely relationship. It is tentatively suggested that, in this environment, *Turbonilla* a is a deposit-feeder, using its buccal pump to draw in the flocculent superficial sediment.

The small spionid polychaete, ?*Spio filicornis*, the ninth most abundant member of the community, utilizes still another mode of feeding. Two large tentacles on the head protrude above the substratum and move over the surface of the surrounding sediment. A ciliated groove situated along the length of the tentacle draws in and carries fine superficial particles to the mouth. The animal therefore is a selective deposit-feeder exploiting only the finer deposited material at the very surface of the sediment.

The remaining 6.5% of the fauna consists of 70 species, none of which make an appreciable numerical contribution to the community. Some members of this group use the same methods of feeding as the common species. However, the significant finding in this study is that definite niche differences can be demonstrated for those few species that make up the vast majority of the fauna.

This study also demonstrates the danger of assuming a carnivorous feeding habit, particularly in the case of polychaetes, from morphology or by feeding experiments in the laboratory. Because of this, two other predatory polychaetes, *Arabella iricolor* and *Lumbrinereis fragilis* were examined to provide data on their food. While both species are of little importance numerically, they are relatively large animals and rank fifth and seventh respectively in regard to biomass (see Table 4). The gut contents of the two specimens of *Arabella* were empty while the single representative of *Lumbrinereis fragilis* contained detritus, numerous centric diatoms and sand grains.

Evidence has now been presented which indicates that biological interaction, or perhaps a better expression would be biological accommodation, plays an important part in the structure of the animal assemblage at station R. It should not be inferred that such a community therefore represents a sharply circumscribed group of species, each with identical distribution patterns. On the contrary, frequently both the sediment ranges of the species and the sediment composition where the maximal numbers are found vary significantly (see Sanders 1958). In fact, the species components of the benthic fauna in Buzzards Bay constitute a continuum varying with the gradual change in sediment composition. Implicit in such distribution patterns is the effect of physical factors. However, as demonstrated in the present study, at a given point (station R) on the sediment spectrum the species structure of the association is similar even when the sampling is done at various times of the year. The interpretation made is that accommodations among the species, biological effects, play a major role in determining the structure of a community. Thus the faunal proportions will vary at different locations on the sediment spectrum in Buzzards Bay and at any point on the spectrum the community structure will be determined by both physical and biological factors. Obviously the gradients of physical factors other than sediment composition play a role. For example, the lamellibranch, *Macoma tenta*, appears to be much more abundant in the same type of sediment in slightly shallower environments. Because of the greater abundance of *Macoma*, it would be interesting to observe what modifications have occurred in the structure of the community at such a location in contrast to that found at station R.

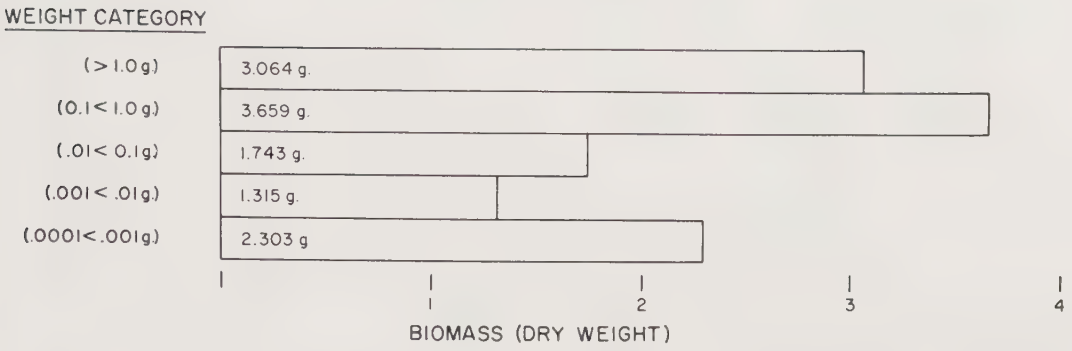

FIG. 2. The relationship of numbers (left) to weight (right) for the benthic community at station R.

For further comments on the subject of biological versus physical regulation see Jones (1950), Hedgpeth (1954) and Longhurst (1958).

Animal numbers and animal weight

Another aspect of the structure of an animal community is the relationship of numbers to weight. It is a common assumption that the smaller the animals the more abundant they will be. Therefore, if the individuals are grouped by number into size or weight categories, a pyramid can be constructed with the smallest size or weight category forming the base and the largest category the apex of the pyramid. Conversely, if the total weight rather than the number is calculated for each of the categories, an inverted pyramid results, with the largest biomass present in the largest size category and the smallest biomass in the smallest size group. However, there is little field evidence in support of this.

The present data lend themselves to the comparison of numbers to weight (Fig. 2). Only the data from the 20 samples with high indices of faunal affinity (*i.e.*, those with similar sediment composition) were used. The intervals chosen were logarithmic rather than arithmetic, thus each category is an order of magnitude larger than the preceding category. Those animals weighing less than 0.0001 g are only partially sampled by a screen with 0.2 mm mesh and therefore those smaller than 0.0001 g are not included in Figure 2. Thus the analysis has validity only for those organisms weighing 0.0001 g or more. Within the range from 0.0001 to more than 1.0 g, there is a constant decrease in numbers from one interval to another (see Fig. 2) which is in agreement with the accepted concept. The average increase in number of individuals is $\times$ 8.5 as one moves from one category to that containing the next smallest animals. A single category, the interval 0.0001–0.001 g, includes 69.4% of the fauna by number.

When the same treatment is applied to total weight or biomass within each of the categories, no trend is evident (see Fig. 3) and the expected inverted pyramid does not materialize. Despite the fact that this situation differs from the theoretical, one should be cautious about generalizing from the results. Obviously the biomass histogram describes the structure of this particular community and to a considerable degree, the form of the histogram reflects the nature of the dominant species. The larger than expected biomass value in the 0.0001 $<$0.001 g interval is undoubtedly due to concentrations of adult *Nucula* and juvenile *Nephthys*. Possibly different kinds of animal communities can be described by characteristic biomass histograms and it may prove feasible to use such histograms as another tool in describing communities.

The present analysis brings out the uncertainty of our knowledge of the feeding habits of many benthic invertebrates and, therefore, a precise definition of number and weight relationships from the trophic aspect cannot be attempted at this time. It

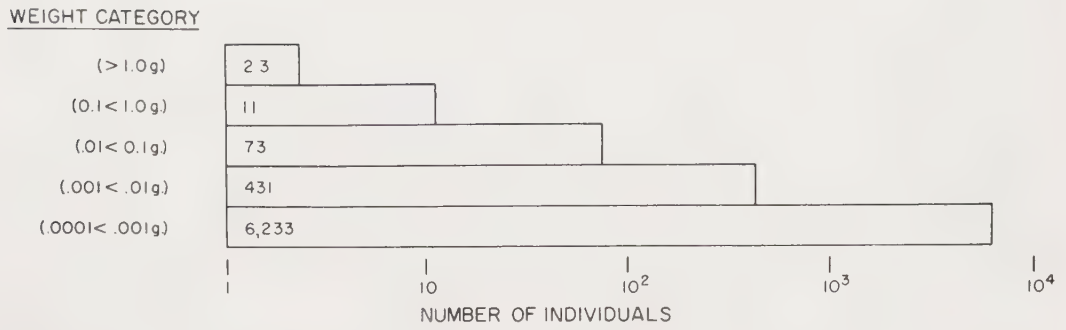

FIG. 3. The relationship of weight categories (left) to biomass (right) for the benthic community at station R.

can be stated, however, that true carnivores make up, at most, about 8% of the fauna by number. The actual percentage is probably much lower.

Finally, some mention should be made of the meiofauna, such as nematodes, kinorhynchs, ostracods and benthic copepods and the contribution it makes to the histograms of numbers and weights at station R. The 4 samples from R station that showed the typical sediment composition in Wieser's study (1960) are considered.

There are about 930,000 meiofaunal animals per m^2, which indicates that they are about a hundred times more numerous than the macrofauna. However, their biomass of 0.3662 g/m^2 is only 1/33 the weight of the macrofauna. The most overwhelmingly abundant group is the nematodes, which comprise 97.66% of the meiofauna by number.

Because it is very difficult to obtain individual weights for such small animals, average weights were used. Therefore the weight ranges within each group cannot be determined and, as a result, it is impossible to assign the proper fraction of each group to its correct weight category.

Wieser found that the average weight of a nematode is 0.00028μg, a kinorhynch, 0.003μg, a benthic copepod, 0.0017μg, and an ostracod, 0.018μg. Thus there is little overlap between the macro- and the meiofauna. Obviously, since the meiofauna consists overwhelmingly of nematodes and the average weight of these animals is appreciably less than the other groups, much of the meiofaunal biomass must be present in the smaller weight categories. Therefore, like the macrofauna, it would seem highly unlikely that a biomass pyramid of the meiofauna at station R would approximate the theoretical inverted form.

In the light of what has been shown regarding animal weights and numbers, it may be convenient here to consider the relative validity of numbers and weights in quantitative faunal studies. Generally speaking, the larger animals are less abundant than smaller animals. Only 13.3 specimens in the largest two categories (see Fig. 2), representing less than 0.15% of the fauna by number, constitute 55.17% of the entire biomass. Since the latter figure represents the average percentage of 20 samples, the effect of these animals on the biomass of individual samples would be much more extreme. It would seem that the presence or absence of the rare, randomly distributed large animals effectively determines the biomass of a sample (see also Sanders 1956). Unless this component is separately assayed, comparative biomass values become relatively meaningless. Because of this difficulty, the writer feels that animal numbers are the more valid measurement providing, of course, that a standard screen with small enough apertures is used so that an adequate number of animals is captured.

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BIOLOGICAL AND GEOLOGICAL OBSERVATIONS ON THE FIRST PHOTOGRAPHS OF THE ARCTIC OCEAN DEEP-SEA FLOOR[1]

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ABSTRACT

The first series of Arctic bottom photographs give the following indications regarding conditions on the Arctic sea floor: Bottom life appears to be less abundant than in the Atlantic Ocean at similar depths. Loose rocks are more numerous. Ripples seem to be less abundant in the Arctic area photographed than they do at comparable depths in the Atlantic. A bottom current of 0.3 to 0.6 cm/sec is indicated from movements of sediment clouds. The area is abundantly supplied with curious short "tracks" of uncertain origin. Small irregular holes in the pictures probably represent holes produced by ice-rafted stones and pebbles.

INTRODUCTION

Arctic drifting Station A, established during the International Geophysical Year by the United States Air Force is a scientific research base floating in the Arctic Ocean on an ice floe of about 10–15 ft in thickness (Fig. 1). During the first year it has drifted at an approximate rate of one to three miles a day within a radius of 300 to 600 miles from the North Pole.

Observational programs in meteorology, aurora, geomagnetism, gravimetry, and oceanography were maintained. The oceanographic program included serial oceanographic measurements, current measurements, biology, seismic depth measurements, coring, and bottom photography (anon. 1957a). The great stability of the floating platform lends itself especially well to photographic operations.

The camera was a modification of the Ewing suspended automatic camera (Ewing *et al.* 1946) Model TM–III, designed and constructed by Dr. Edward Thorndike, Professor of Physics at Queens College, New York, and Research Associate at the Lamont Geological Observatory. The camera was lowered on a one-eighth inch stainless steel cable by a gasoline-driven winch, fitted with a small spring-type dynamometer. Bottom contact was determined from acoustic signal (pinger) and from the dynamometer indication.

A total of 140 exposures were taken at the bottom at two different locations by Frans van der Hoeven, then Chief Scientist at Station A. To our knowledge these are the first bottom photographs ever taken of the sea floor of the central Arctic Ocean.

The geophysical program at Station A was directed by Professor Jack Oliver. The Arctic camera project was initiated by Maurice J. Davidson. While the pictures were taken, the Station was under the command of Lt. Col. Helmuth E. Stromquist, USAF, and we acknowledge the commanding officer and his men for their aid in getting the camera in operation. We gratefully acknowledge financial support of the Air Force Cambridge Research Center of the Air Research and Development Command. Valuable advice was received from Prof. Thorndike concerning the area of the bottom covered by the various exposures.

Camera station DSA–1. Position: Lat. 83° 49′N; Long. 165° 05′W. Depth 2997 meters, wire sounding. Ninety-five exposures. Date 12–13 December, 1957; on the south flank of the newly discovered Alpha Rise. Bottom contact was indistinct, camera was laid on the bottom for much of the time; many of the pictures were taken with the camera in essentially the same position. Eighty-six exposures were made covering 30 different bottom sites.

Camera station DSA–2. Position: Lat. 83° 34′N; Long. 162° 15′W. Depth 2300 meters by wire sounding. Time 2120 GMT to 2340

[1] Lamont Geological Observatory Contribution No. 411.

FIG. 1. Arctic Ocean. Locations of sea floor photographs shown by dots 1 and 2. The 200, 2000, 3000, 4000 and 5000 m isobaths are shown. The three major transoceanic topographic features are from east to west. A, the Mid-Oceanic Ridge; B, the Lomonosov Ridge, and C, the Alpha Rise. The photographs were taken on the Alpha Rise.

GMT; 20 December, 1957. This location is also on the south flank of the newly discovered Alpha Rise (Anon. 1957b). Seventy-four exposures were made covering 55 different bottom sites.

BIOLOGY

Life in general and the evidence for life seems rather sparse; however, one series of exposures (DSA–1–3 through DSA–1–22) all taken at about the same place, did show an erect bryozoan colony attached to the mud, an actinarian attached to the edge of an uncovered rock, what appears to be a cup-shaped sponge on the mud, and possibly a holothurian or gastropod on the surface of the mud. The kinky or angular elongate "tracks" which are not connected with one another do not seem to be biogenic (Fig. 2A) although it is difficult to imagine another source other than biologic. They might have been produced by some vagrant benthont such as a bottom feeding fish. The mounds that are present in some exposures are probably not biogenic because of the absence of a central cavity (*cf.* Fig. 4D from the Atlantic). These mounds seem to represent rocks covered by sediment. The general picture is one of an area with little life. The holes do not seem typical of holes produced by animals due to their irregularity and angularity. One would expect worm-holes to be in more regular patches, (*cf.* Fig. 2B from the Atlantic) often with tubes protruding. Such is not the case with these. A clam burrow would show certainly a characteristic fringe of sediment around the hole and, in many instances, a pair of holes, one for each siphon. The holes produced by a covered asteroid would be sym-

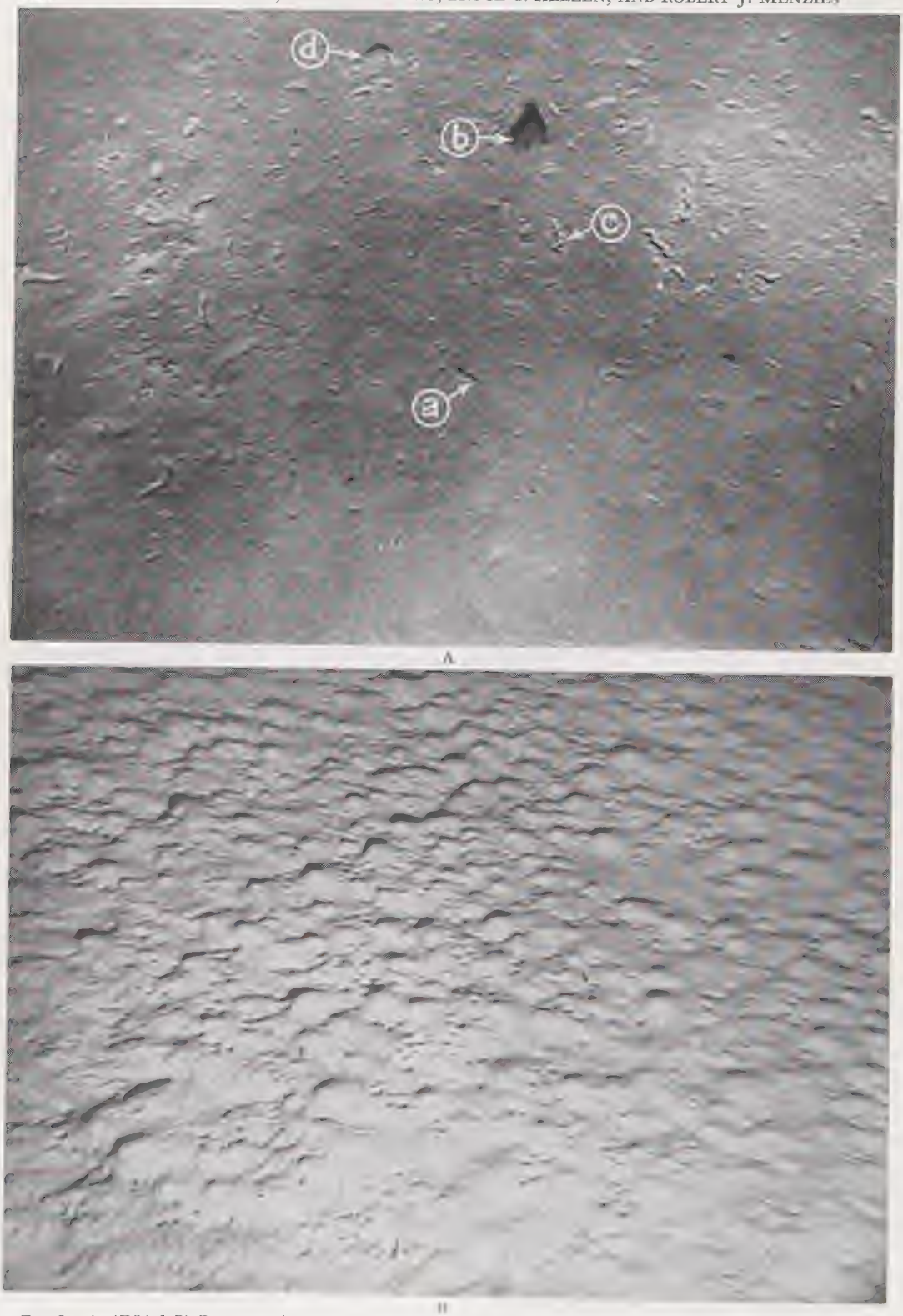

FIG. 2. A. (DSA-1-5) Bottom at Arctic Station A, 2997 m depth, Latitude 83°49′ N, Longitude 165°05′ W. Note sessile bryozoan colony (a), actinarian attached to rock (b), sponge (c) and gastropod (d), and "tracks" of unknown origin. B. Mounds and holes from Atlantic Station THETA 1-39-95, Latitude 28°07′ N, Longitude 14°09′ W, depth 800 m.

FIG. 3. A. Rock and pebbles on bottom at (DSA-2-61) Arctic Station A, 2370 m depth, Latitude 83°34′ N, Longitude 162°15′ W. Note absence of life. B. Rocks covered with sessile animal life, VEMA 4, 14-36, from Latitude 35°12′ N, Longitude 15°22′ W, and 1935 m depth. A seamount in the eastern Atlantic.

FIG. 4. A, *DSA-1-42* (Argo's "Tracks") from Arctic Station A, at Latitude 87°49′ N, Longitude 163°05′ W, 2367 m depth. B, Mounds from Arctic Station A, *DSA-2-9*, at Latitude 85°54′ N, Longitude 162°15′ W, depth 2310 m. C, Aerial tracks from THETA 1-30-64, Latitude 28°07′ N, Longitude 14°09′ W, depth 2310 m. D, Aerial-produced mounds and holes from THETA 1-30-67, Latitude 28°07′ N, Longitude 14°02′ W, depth 2310 m.

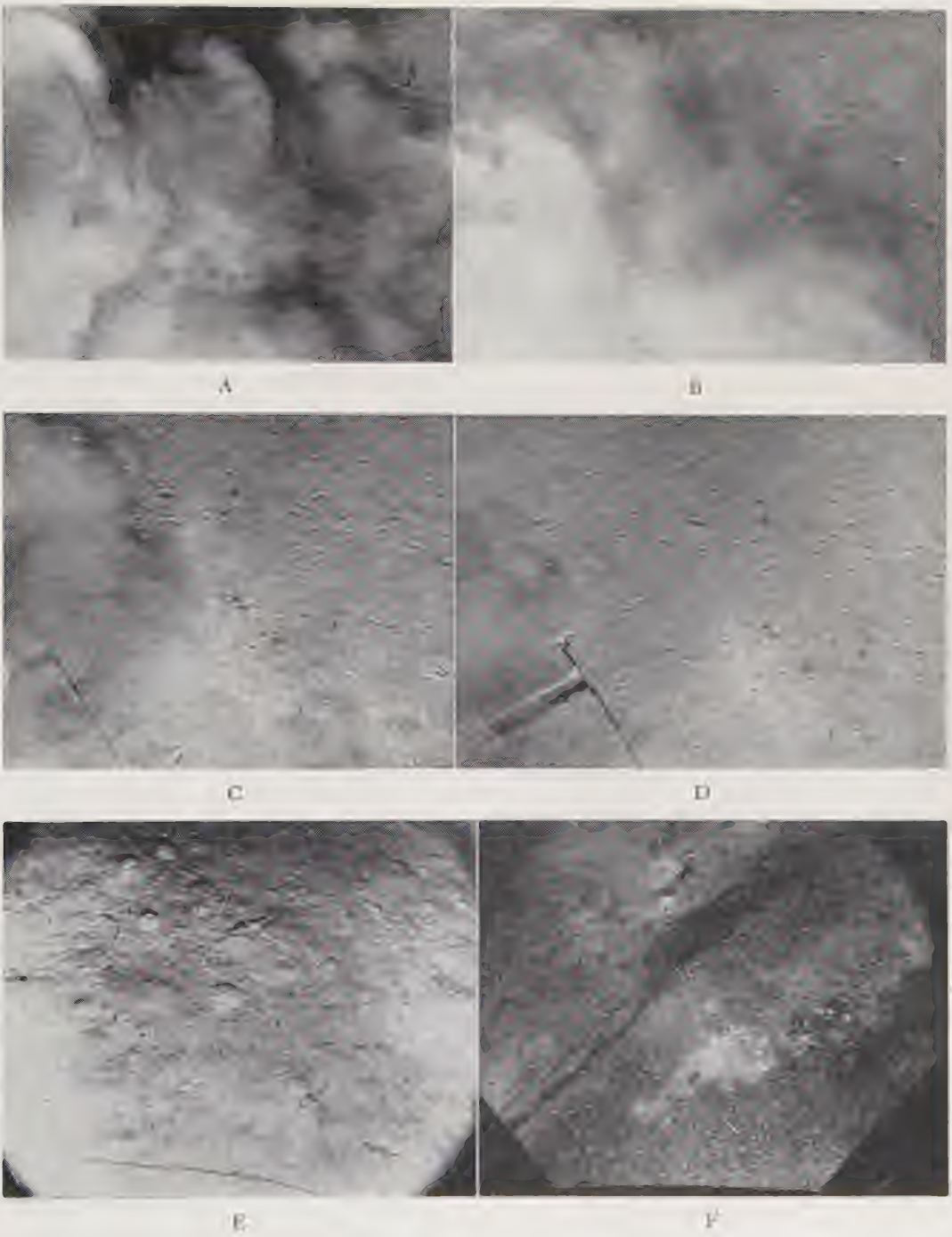

FIG. 5. A.–D. (DSA-2-62 to 65) Movement of sediment cloud across camera field of view, Latitude 83°34′ N, Longitude 162°15′ W; 2370 m depth. Sediment moves to the left and toward the camera against a fixed bottom background, finally revealing impressions, made by the camera on the bottom, in a previous position. E. Buried sea-star from THETA I-13-31; 4725 m depth, Latitude 45°42′ N, Longitude 20°38′ W. F. Atlantic ripple marks from VEMA 4-16-18, 1980 m depth, Latitude 35°07′ N, Longitude 13°04′ W.

metrical (see Fig. 4C from the Atlantic.) None of these features are revealed in the Arctic photos.

ROCKS

The abundance of rocks on the Arctic ocean floor is one of the more striking features of these photographs. Only three out of 30 sites in DSA-1 failed to show exposed rocks. All 55 sites in DSA-2 revealed rocks. One or two large rocks (about 10 cm diam.) are seen in most of the photos. In addition, many smaller rocks (about 1 cm diam.) are shown, especially by closeups when the camera rested on the bottom. In most cases the rocks are clear of sediment, but in some exposures, partial burial by fine-grain sediment is shown. One photo, Fig. 3A, shows a tabular boulder which is one-half a meter wide and which must exceed one meter in length. This large rock is partially buried and on top of its covering of sediment smaller rocks are found. Evidently some of these rocks have been in position on the ocean floor for a long period and others are continuing to be emplaced. All rocks shown are dominantly angular and the larger ones are tabular.

Examination of dredged material from a nearby area (84° 40′N, 170°51′W) reveals an extremely heterogeneous group of pebbles consisting of shale, sandstone, quartzite, white quartz, rose quartz, muscovite, gneiss, etc. All are angular to sub-angular. One shows glacial striae. The angularity, heterogeneity, random distribution of the rocks in the photo and general lack of ripple marks all suggest that the rocks were rafted by ice to their present position. The partial burial of some rocks indicates that the rafting has been taking place over a long period of time.

RIPPLE MARKS

Prominent ripple marks are not shown on any of the photographs. Exposures DSA-1–21 and DSA-1–22 have features which may be interpreted as ripples, but this is not certain. Both photos were taken at low angles of a site which did not reveal ripples when photographed at the normal camera angle.

BOTTOM CURRENTS

Evidence for relatively high velocity bottom currents comes from an unusual and significant source. The camera was accidentally allowed to sit on the bottom several times and took many photographs of the same area of ocean floor. Against the background of the bottom, the mud cloud, stirred up by the camera, drifted while it was being photographed at regular intervals. Two good sequences were obtained (DSA–1–8 to DSA–1–16 and DSA–2–66 to DSA–2–69). The camera takes pictures at approximately 35 second intervals when allowed to rest on the bottom. This information, together with the dimensions of the area photographed, approximately 1.1 m × 0.8 m, allows us to estimate bottom current velocity. In DSA–1–10 through DSA–1–14 the mud cloud raised by the cable which coiled on the bottom drifts across half the picture area (Fig. 5A-D). This gives a velocity of about 0.3 cm/second. In DSA–2–67 through DSA–2–70 the mud cloud raised by the camera contacting the bottom crosses nearly the whole photo area. A velocity of about 0.6 cm/sec is indicated.

The possibility that the sediment cloud had settled instead of being moved by current was considered. Experimentation indicates this is not the case. A sample of bottom sediment from 83°53′N, 168°42′W was stirred in sea water and allowed to settle. The material was extremely fine grained and at least one-half hour was required to clear a 30 cm column to transparency again. Thus it seems unlikely that the sediment cloud in the picture could have settled in a period of only several minutes, which is the length of time taken for it to disappear from the camera's field.

HOLES

All of the pictures show shallow depressions or holes on the ocean bottom. Some of these holes are round, others are linear or linear with small kinks and angular bends. The round holes average about 1 cm in diameter. The linear holes vary from 1 to 10 cm in length and are about one-

fourth to one-eighth as wide as their length. The pictures taken at Station 1 show a greater abundance of holes than those taken at Station 2.

The holes with the sharpest outline, apparently the most recent ones, all have a raised ridge around the edge.

The round holes probably are due to the fall of ice-rafted rocks. Similar holes were produced experimentally by dropping pebbles into a seawater tank having a sediment floor. The linear holes are more difficult to explain. A biological explanation is possibly indicated but no wholly satisfactory mechanism has yet been suggested.

MOUNDS

Camera Station 2 differs from Camera Station 1 in showing numerous mounds in several pictures (Fig. 4B). The mounds are all roughly similar, being shallow domes of several centimeters in diameter. It is believed that these mounds are primarily sediment-covered rocks. The absence of axial holes, characteristic of biological holes, supports this conclusion.

BOTTOM SEDIMENT

Except for rocks and pebbles, the bottom surface sediment is probably composed of foraminiferal lutite. The sediment clouds stirred up by the cable and camera striking bottom gives evidence that the sediment is soft and fine-grained. Below the fine, unconsolidated few centimeters of surface layer there must exist a fairly firm layer as shown by shallow marks left by the cable and camera when they struck bottom, (DSA–1–8 to DSA–1–16 and DSA–2–68, 69).

Surface sediment as determined by sampling in nearby areas is a brownish, weakly foraminiferal lutite. A bottom core was taken at DSA–2 but an analysis is not yet available.

COMPARISON OF ARCTIC AND ATLANTIC PHOTOS

The irregular holes shown in Figure 2A from the Arctic at a depth of 2997 m should be compared with the regular and clumped worm holes shown in Figure 2B from the Atlantic at 800 m depth. The irregular and random distribution of the holes shown in the Arctic bottom photograph argue that they are not biologic in origin.

Typical animal tracks from the Atlantic at 2310 m are shown in Figure 4C where the continuity of the tracks is quite unlike the irregular, angular and discontinuous "tracks" shown in Figure 4A (DSA–1–41) from the Arctic at 2197 m.

The mounds of Figure 4B from the Arctic are unlike typical animal-produced mounds from the Atlantic Figs. 2B and 4D which have a more angular peak and a central or axial cavity. Often in Atlantic photos one sees the pentangular holes produced by covered asteroids. This is shown in Figure 5E from 4725 m depth.

An exposed tabular rock which is from the Arctic is virtually devoid of life (Fig. 3A) should be compared with an exposed rock covered abundantly with (Fig. 3B) sessile animal life.

Ripple marks are frequently encountered in Atlantic bottom photos Fig. 5F. In the Arctic photographs no distinct ripples are shown. Since not all Atlantic bottom photos show ripples, the apparent absence of ripples at two Arctic localities is hardly conclusive proof of their absence in the Arctic.

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SOME OBSERVATIONS OF TURBIDITY IN BRITISH COLUMBIA INLETS[1]

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ABSTRACT

Measurements have been made by a light scattering method of the optical turbidity of the waters in some typical British Columbia inlets with depths to 700 m. (The optical turbidity here used is the extinction coefficient or fractional reduction in light intensity per meter length due to scattering.) The major contribution to the turbidity in the large inlets is the minerogenic material brought in by rivers. Therefore those inlets with rivers originating in glaciers exhibit the highest turbidity values and there is a marked seasonal variation. In the surface layers, values recorded for turbidity range from 0.2 m^{-1} in winter to 35m^{-1} in summer with a marked decrease from head to mouth of the inlet. The main body of water in an inlet is usually fairly uniform in turbidity at 0.1 to 2m^{-1}. (For comparison, double distilled water has a turbidity of 0.024m^{-1} for light of wavelength 5460 A in air.) Particle sizes average about 20μ diameter in summer and 8μ in winter, with little material less than 2μ in diameter. An increase in turbidity near the bottom is common and may be due to tidal currents but evidence suggests that turbidity currents originating at the inlet head may be common and contribute to the bottom water turbidity.

INTRODUCTION

The British Columbia coast is a typical example of a fjord coast, being rocky and indented with numerous inlets of length up to 160 km and average width from 0.9 to 5.5 km. The average depth is about 330 m while the maximum known is 730 m. The inlets have sills which are shallower than the maximum basin depth and vary from 15 to 350 m except for a few small inlets. A significant fact is that even the shallowest sills are considerably deeper than the low salinity surface layer, and stagnant conditions such as are found in many Norwegian fjords are uncommon in British Columbia. One characteristic of the inlet morphology is the occurrence of very flat bottoms inside the sills of some inlets.

The oceanographic characteristics of the mainland coast inlets have been under study for several years and a fair picture of the distribution of salinity, temperature and dissolved oxygen content has been assembled for the summer months, with some information on the annual cycle in two or three inlets. Bute Inlet, described by Tabata and Pickard (1957), is typical.

The majority of the inlets have a large spring and summer runoff of fresh water from rivers which originate in glaciers or snowfields. Consequently the general pattern of salinity distribution is of a low salinity surface layer overlying higher salinity deep water. At the head (inland end) of such inlets there is a well defined salinity structure, with a sharp halocline and thermocline. The surface layer is 3 to 10 m deep, depending on the inlet and the time of year. The surface layer moves seaward and picks up salt water from below as it does so. As the inlet mouth (seaward end) is approached the difference in salinity between surface and deep water decreases and the halocline becomes less marked. There is a seasonal variation in surface salinity from 0 to 10‰ in summer to 25 to 29‰ in winter, the lower values occurring toward the inlet head. In the inlets with smaller runoff the halocline is less marked, even at the inlet head. The salinity in all inlets reaches at least 90% of the deep water value by a depth of 20 m. The surface temperature varies from about 5°C in winter to 10 to 15° in summer in the large runoff inlets, and may rise to 24° in the small runoff inlets.

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The deep water salinity and temperature vary from 30.7‰/8.3°C in the southern inlets to 33.2‰/6.3°C in the northern ones. Seasonal fluctuations of temperature and salinity are generally not conspicuous at depths greater than about 100 m. There does not seem to be any regular seasonal variation of these characteristics in the deep water, 300 to 700 m, but irregular year to year changes do appear to occur.

Dissolved oxygen values are usually close to or above saturation, or 7 to 10 ml/L, in the surface layers and decrease to 2.5 to 4.5 ml/L in the deep water.

To supplement the above information, measurements have recently been extended to include optical turbidity. The object is to investigate its use as an additional water characteristic for tracing water movement, and to try to learn something of the distribution and character of the particulate material in the water. The measurements have been made in a few typical inlets in the southern coast of British Columbia. Jerlov (1953) has described results of particle content measurement in fjords, and Burt (1955a,b) has described results of turbidity measurements in Chesapeake Bay. Both of these regions are much shallower than the B. C. inlets.

METHOD

Samples were collected with reversing water bottles, most of the work being done with bottles coated internally with ceresin. Tests of bottles without the coating showed turbidity values 0.05 to 0.1 m^{-1} higher than the treated bottles. This error would have been significant only in a minority of the samples measured. The turbidity was determined immediately on shipboard by measuring the light scattered by samples by means of an Aminco Light Scattering Microphotometer. This is a production item based on that described by Oster (1953) and uses a photomultiplier detector arranged to measure transmitted light or light scattered through angles up to 147°. A light scattering method was used, rather than a transmission method, in order to investigate how much information could be

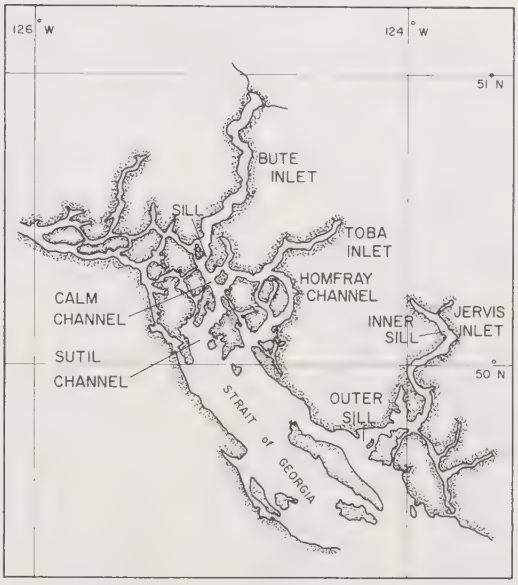

FIG. 1. Outline map of region of turbidity study in southern British Columbia.

obtained on the character of the particulate material in the water. The potentialities of light scattering techniques are discussed at length by Jerlov (1955), Stacey (1956), and Van de Hulst (1957).

The optical characteristic of the water which will be used for description here will be the turbidity τ defined by:

$$I = I_0 \cdot e^{-\tau L}$$

where I_0 and I are the incident and emergent light intensities of a parallel beam of light passing through a column of water of length L. The unit used for τ will be reciprocal meters (m^{-1}). In this unit the turbidity of double distilled water is about 0.024 m^{-1} for light of wavelength (in air) of 5460 A.

The interpretation of the scattered light measurements was based on frequent calibration of the instrument by means of 'Ludox' colloidal silica suspension as described by Oster (1953). Measurements were made of the light scattered at 45° to the forward direction with green light (5460 A in air) for all samples, for blue (4360 A) and yellow (5780 A) light for alternate samples. For selected depths and stations measurements at intervals of 10° in scattering angle were also made to obtain

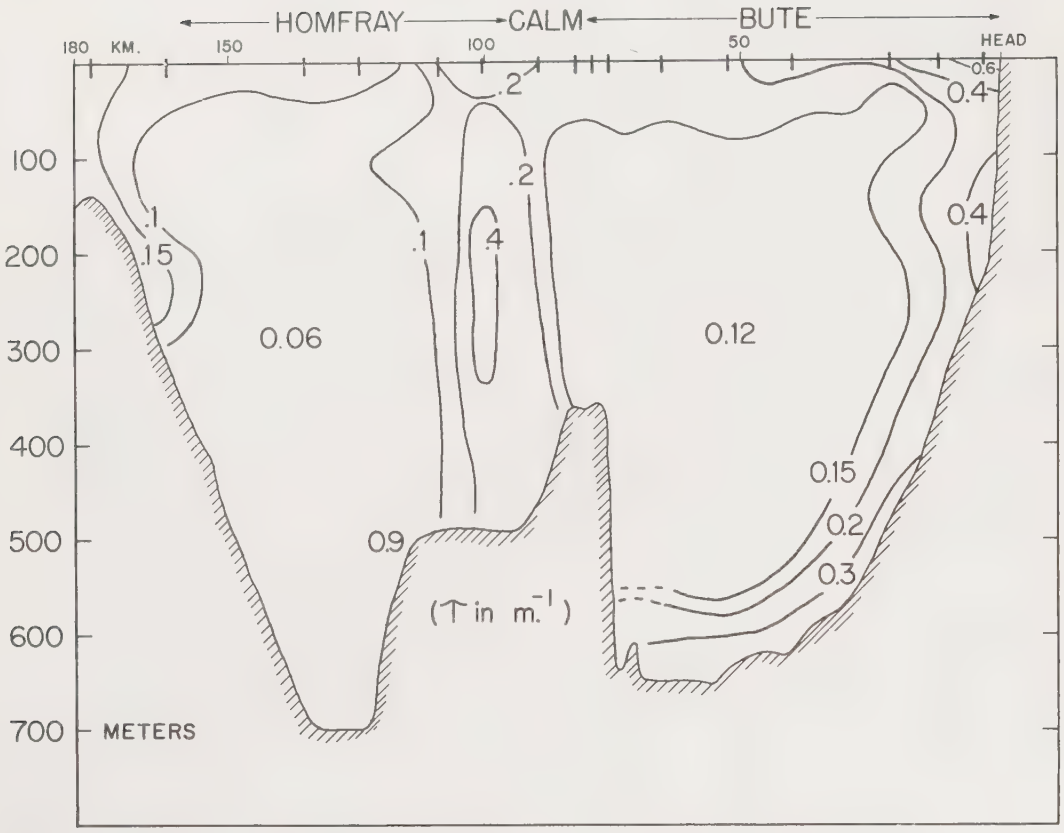

FIG. 2. Distribution of turbidity in winter in longitudinal vertical section along Bute Inlet and connecting channels. Station locations are indicated by bars on top line.

a polar diagram of scattered light intensity. A number of water samples were filtered and the filter retained material examined under a microscope.

The reduction of the photometer readings to turbidity values was based on the assumption of single scattering in the sample. According to Van de Hulst (1957, p. 6) single scattering can be assumed up to an optical path (product of turbidity times geometrical light path in the sample) less than 0.1, and that multiple scattering must be assumed to occur for an optical path of greater than 0.3. In the present observations this value was reached for a turbidity of about 8 m^{-1}. In consequence the stated values for the highest turbidities reported here are probably too high. Since there is no certain and convenient way to correct for multiple scattering and since values of turbidity which require correction occur only in summer at the head of some inlets in a very small fraction of the total water volume, no attempt has been made to correct them. A few experiments on high turbidity samples in which scattering measurements of the turbidity were supplemented by transmission measurements suggested that the values for turbidity can be approximately corrected by multiplying by a factor decreasing from 1 at 8 m^{-1} to 0.5 at 35 m^{-1}.

RESULTS

Distributions of turbidity will be described for Bute and Jervis Inlets (Fig. 1) which are basically similar in morphology. They differ in that Bute has a large river runoff from glaciers in spring and summer, while Jervis has a much smaller runoff with little or no glacial contribution. The series of measurements were made during seven

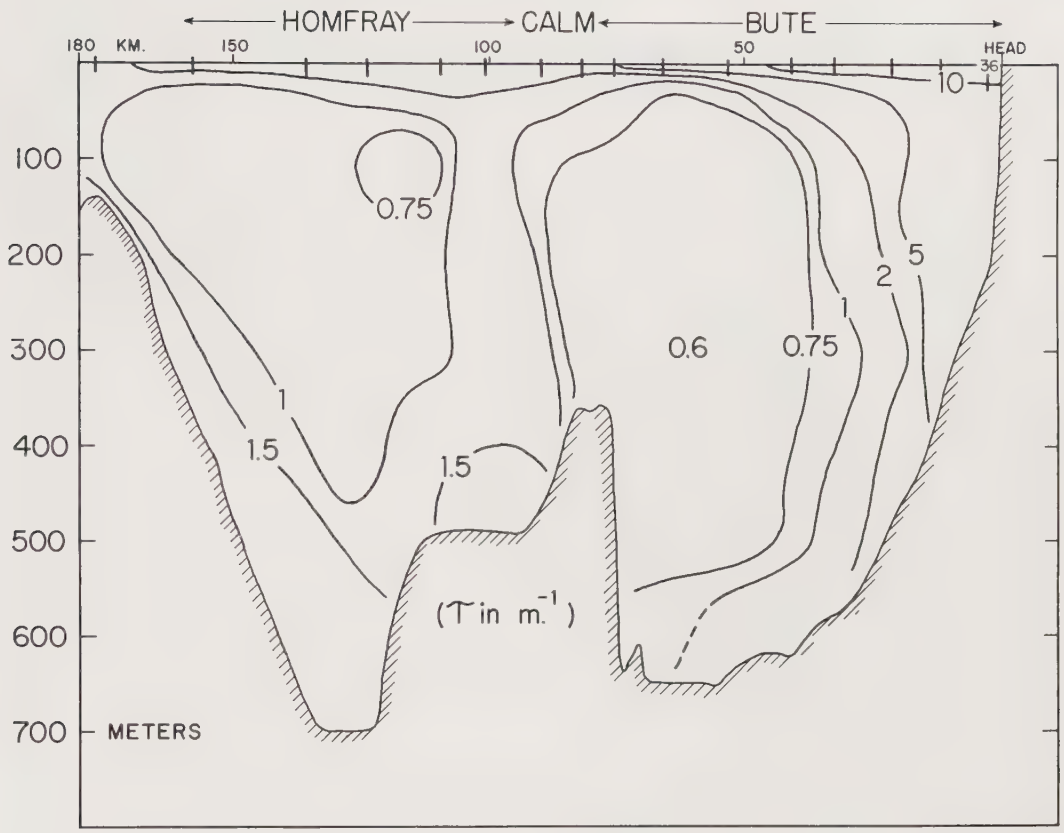

FIG. 3. Distribution of turbidity in summer in longitudinal vertical section along Bute Inlet and connecting channels. Station locations are indicated by bars on top line.

cruises from May, 1957 to June, 1958. During this period a marked seasonal variation was observed and it is believed that conditions during this period were substantially typical. The turbidity was generally at a minimum in winter and a maximum in late spring or early summer. Figures 2 to 5 show longitudinal sections representing these conditions.

Bute Inlet—February, 1958, Figure 2

Surface values of turbidity ranged from 0.7 m^{-1} at the head to 0.2 m^{-1} at the mouth. A marked turbocline associated with the thermocline and halocline was present near the inlet head. The main body of the inlet water from 100 to 550 m depth was fairly uniform in turbidity at about 0.12 m^{-1}. In the deepest parts between 550 and 650 m the turbidity increased to values as high as 0.4 m^{-1}, the value generally being greatest near the bottom and near the inlet head. In Sutil Channel the bulk of the water had a turbidity of 0.23 m^{-1}. In Homfray Channel the main mass of the water had a turbidity of 0.06 m^{-1} (only about three times that for double distilled water), with a small increase near to the bottom.

One peculiarity was that a region of uniformly high turbidity from top to bottom in Calm Channel was observed during this February, 1958, cruise but was absent in March. The material appeared from microscope examination to be chiefly minerogenic in character. Another feature of the region outside the inlets was a discontinuity in turbidity in the horizontal direction at all depths between the high turbidity Toba Inlet water and the low turbidity Homfray water.

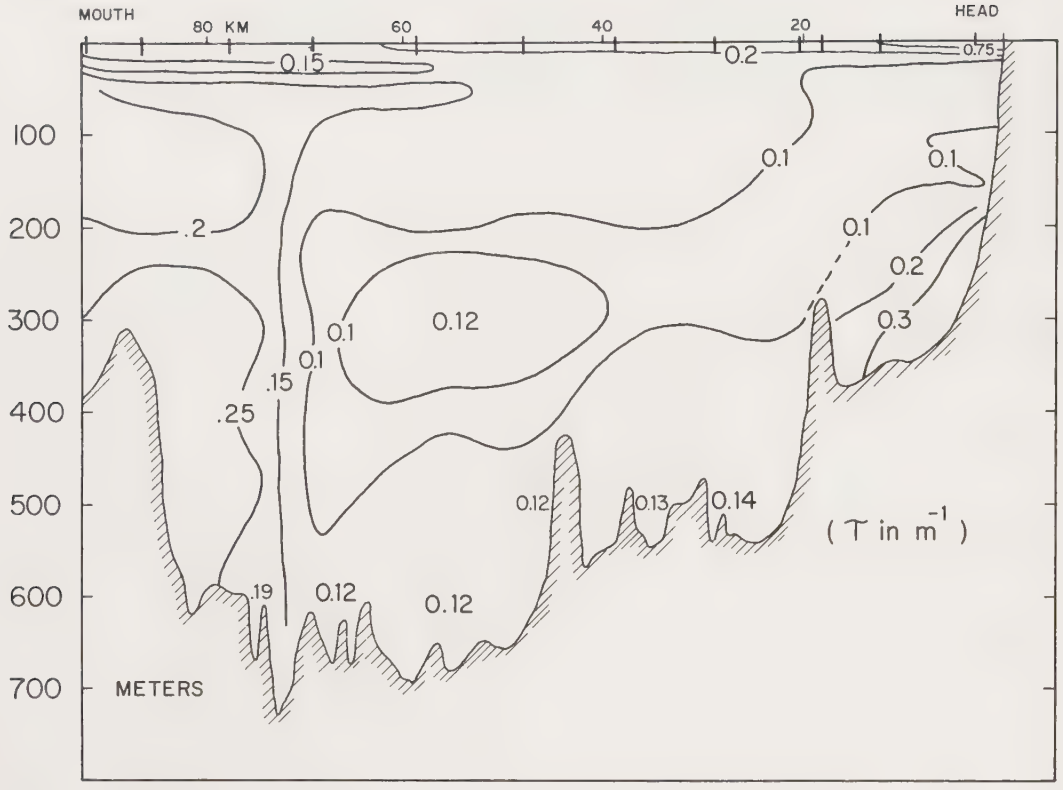

FIG. 4. Distribution of turbidity in winter in longitudinal vertical section along Jervis Inlet. Station locations are indicated by bars on top line.

Bute Inlet—June, 1958, Figure 3

Surface layer values of turbidity decreased from 36 m^{-1} at the head to 7 m^{-1} at the mouth, the longitudinal rate of decrease being small in the seaward one third of the inlet length. There was pronounced horizontal stratification, and a turbocline existed close to the halocline, although the finite size of the water bottles makes it difficult to be specific about the position of the halocline etc. The turbidity decreased by 3.5 to 2 times across this turbocline. There was some horizontal stratification below the surface layer in the inner half of the inlet but in the outer half the turbidity was uniform at about 0.6 m^{-1} between 100 and 550 m deep. Again there was an increase by a factor of 1.5 to 2.5 in the bottom water.

In Sutil Channel the water to 100 to 150 m depth had the same turbidity as that in Bute (0.6 m^{-1}) but values were larger near the surface and the bottom. In Homfray Channel the surface layer had a turbidity of 3.5 m^{-1}. Between 50 and 150 m the value was lower at 0.8 m^{-1} while between 200 and 600 m it increased to 1.2 to 2.0 m^{-1}.

There was again a sharply defined turbidity region in Calm Channel, as in February, where a uniform turbidity of 1.3 m^{-1} was observed from 100 to 400 m depth. However, an appreciable amount of material present at this time in June was of biological origin in contrast to the February situation. There was essential continuity between Toba and Homfray mid-depth water in contrast to the winter situation.

Jervis Inlet—February, 1958, Figure 4

Surface values of turbidity near the head were 0.85 to 0.95 m^{-1} and decreased to 0.14 m^{-1} at the mouth, while the turbocline was not as sharp as in Bute. In the main basin between the surface layer and 300 m (outer sill depth) the turbidity was uniform at 0.1

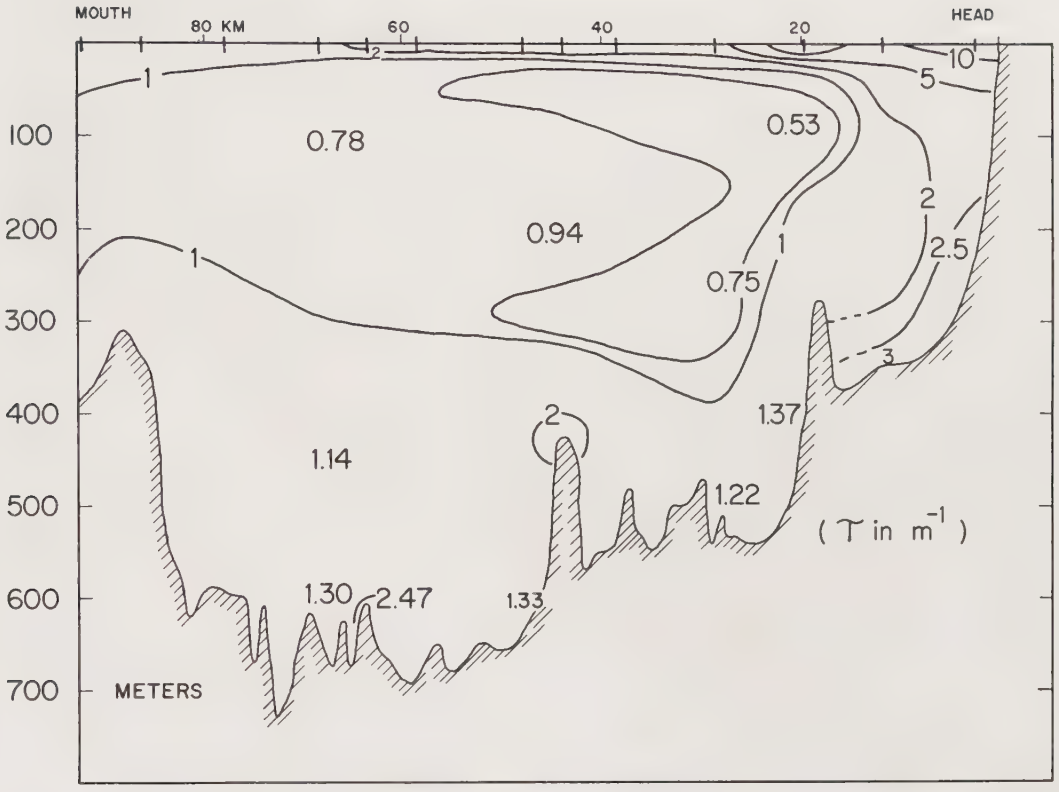

FIG. 5. Distribution of turbidity in summer in longitudinal vertical section along Jervis Inlet. Station locations are indicated by bars on top line.

m^{-1} with some increase toward the mouth. The deeper water in the main body of the inlet had a higher value ($0.2\ m^{-1}$) but there was no marked increase near the bottom. In the inner basin the values did increase near the bottom to about $0.45\ m^{-1}$.

Jervis Inlet—June, 1958, Figure 5

Surface layer turbidities ranged from 12.8 m^{-1} near the head to $2\ m^{-1}$ at the mouth, *i.e.* about one third of the values in Bute at the same time. The turbocline was sharper than in winter, and comparable to that in Bute, although the halocline was much less sharp than in Bute. Between 50 and 300 m the turbidity at the head was $1.0\ m^{-1}$ decreasing to 0.6 and then increasing to $0.9\ m^{-1}$ at about mid-inlet. The value then remained the same to the mouth. In the inner basin the values near the bottom rose to $3.0\ m^{-1}$. In the main basin the value was about $1.0\ m^{-1}$ while higher values of $2.5\ m^{-1}$ were observed in the deepest part of the inlet and up to $2.2\ m^{-1}$ over some of the pinnacles or ridges of the inlet bottom.

THE NATURE OF THE SUSPENDED MATERIAL

Polar diagrams of the scattered light generally showed predominantly forward scattering with a broad minimum between 100° and 120°. The polar diagrams were of substantially the same shape for all samples from the most turbid to the least, and there was little difference with the wavelength of light used. Figure 6a shows an example of a polar diagram of the light scattered by a water sample of high turbidity while Figure 6b shows one for low turbidity water. The predominant forward scattering suggests a preponderance of relatively transparent material of size large compared to the wavelength of light used. Some of the back scattering may be due to white opaque

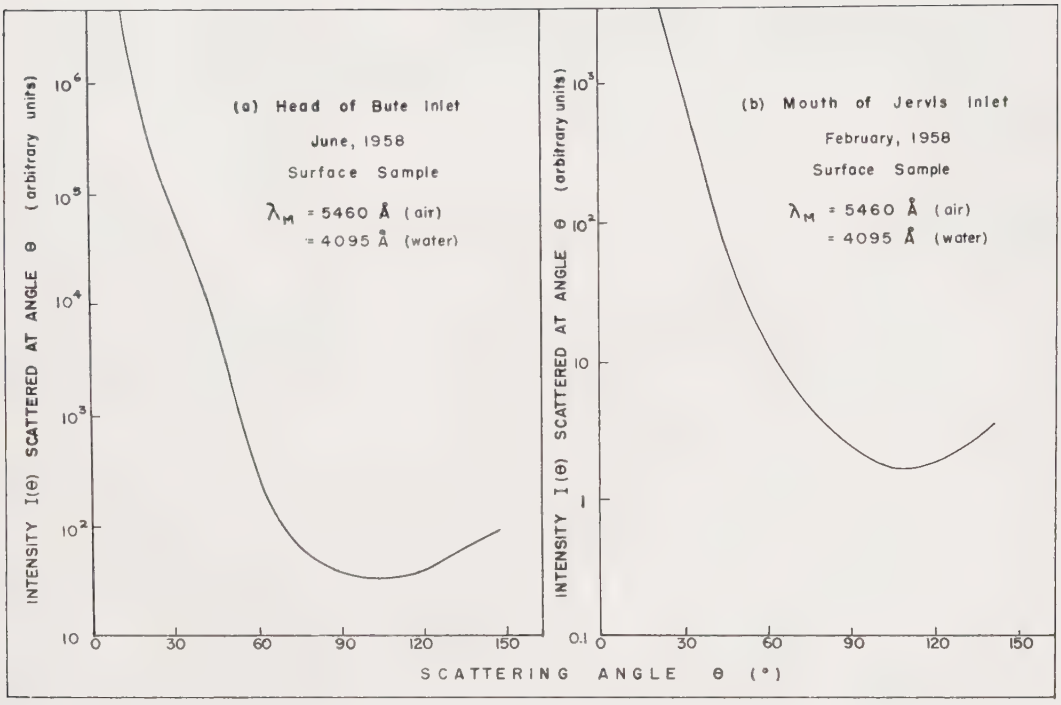
(a) Head of Bute Inlet
June, 1958
Surface Sample
λ_M = 5460 Å (air)
= 4095 Å (water)
(b) Mouth of Jervis Inlet
February, 1958
Surface Sample
λ_M = 5460 Å (air)
= 4095 Å (water)
INTENSITY I(θ) SCATTERED AT ANGLE θ (arbitrary units)
SCATTERING ANGLE θ (°)

FIG. 6. Polar diagrams of light scattered by (a) water of high turbidity, (b) water of low turbidity.

particles or to multiple internal reflection of light in transparent material.

Measurements were made on Millipore-filtered water samples from the upper low salinity ($S<3‰$) layer. The scattering for the filtrate was only about 10% greater than that for double distilled water, indicating that the contribution to scattering by particles of diameter less than 0.5μ, the filter pore-size, was small. There did not appear to be any effect which could be attributed to dissolved colored matter such as "yellow substance."

Measurements of the depolarization ratios for samples with τ less than 2.5 m^{-1}, to reduce multiple scattering effects, gave average values of:

$$\rho_u = 0.055 \pm 0.005$$
$$\rho_v = 0.34 \pm 0.009$$
$$\rho_h = 0.015 \pm 0.004$$

The depolarization ratios ρ represent the deviation from complete polarization of light scattered at 90° as follows:

$\rho_u = H_u/V_u$, for unpolarized incident light,

$\rho_v = H_v/V_v$, for vertically polarized incident light,

$\rho_h = V_h/H_h$, for horizontally polarized incident light,

where H and V represent the intensities of light polarized in the horizontal and vertical planes respectively.

The significance of different combinations of numerical values of the depolarization ratios is summarized by Oster (1948). The above results indicate that the suspended material in the water is both large in size and optically anisotropic in character.

A number of samples from the more turbid surface layers were filtered with Millipore filters and the retained material examined under a microscope. In the most turbid samples in June, diameters ranged from 0.75μ to 49μ with a geometric-mean diameter D_g of $16.7 \pm 1.5\mu$, and the material was about 99% inorganic. Corresponding values for the surface layer water in February were from 0.5 to 15μ with a value of D_g of $7.3 \pm 1.5\mu$, while about 10% of the sample was composed of marine organisms.

TABLE 1. *Comparison of particle sizes and volume concentration in different localities*

	Geometric Mean Diameter	Volume Concentration
Bute Inlet, B. C.	up to 17 μ	1 to 105 ppm
Chesapeake Bay	1.2μ	1 to 60 ppm (Burt 1955b)
Eastern Tropical Pacific (Surface)	1 μ	(Burt 1958)
Eastern Tropical Pacific (400 m)	0.4μ	

Samples taken at several depths in the water column at the head and mouth of Bute Inlet had the following mean diameters:

Bute Inlet	February	June
Head:	10 $\pm$ 1.5μ	17 $\pm$ 1μ
Mouth:	7 $\pm$ 2 μ	8 $\pm$ 1μ

The summer size values correspond well with values for particle sizes in bottom sediments determined by Toombs (1956).

The volume concentration (C_v) of the inorganic material in the most turbid sample was calculated to be 105 ppm and the weight concentration (C_w) about 285 mg/L assuming the material to be granitic with density of 2.65 g/cc. The data for the more turbid summer samples may be approximated by the linear relationships:

$$\left.\begin{aligned}\tau &= 0.32\ C_v + 1.3 \\ &= 0.12\ C_w + 1.3\end{aligned}\right\} \text{ for } \tau > 8\ m^{-1}$$

using the above units for the numerical values of C_v and C_w. For less turbid samples:

$$\left.\begin{aligned}\tau &= 0.27\ C_v + 0.03 \\ &= 0.10\ C_w + 0.03\end{aligned}\right\} \text{ for } \tau < 3\ m^{-1}$$

The above size etc. data are compared with those for other regions in Table 1.

DISCUSSION

The high turbidity in the surface layers with lower turbidity in the main water body are broad features of the distribution which were known or anticipated from the general character of the region and from previous results (*e.g.* Jerlov 1953). It is believed that the present description is the first for a deep fjord-type water body and the first to include quantitatively the seasonal variation feature.

The concentration of suspended material in summer is large compared to that in the open sea but not compared to such regions as the vicinity of the Mississippi. A rather bold estimate of the rate of deposition of sediment from the difference between summer and winter concentrations suggests a figure of about 35 cm depth per 1000 years averaged over the whole inlet. This does not seem to be an unreasonable figure; since there is some indication that the accumulation of bottom material is concentrated in certain regions, the actual rate is probably greater than this.

The increase in turbidity in the bottom water was reported by Jerlov (1953) in the shallower Gullmar Fjord, and attributed to the stirring action of currents. In the deeper B. C. inlets the existence of currents near to the bottom is less certain, though measurements made in Knight Inlet (Pickard and Rodgers 1959) show that currents of tidal period of a few centimeters per second do occur at 50 m from the bottom in a depth of 350 m. The turbidity data may perhaps be taken as evidence that the currents do, in fact, reach to the bottom. An alternative or additional possibility is that turbidity currents starting at the steep mud banks near the inlet head may flow along the bottom and carry material along the inlet. It has been argued (Pickard 1956) that the very flat bottoms inside the inlet sills are a consequence of turbidity current transport of material from the head and of subsequent deposition in the inlet basin. Whether such turbidity currents would be large infrequent affairs, or small frequent ones is unknown. The continued occurrence of the turbid deep water may be taken as evidence in favor of the latter possibility. The fact that there is some degree of sorting in the bottom sediments with size decreasing toward the inlet mouth would be in favor of the small turbidity current hypothesis rather than the large one. In this

connection it may be noted that in Jervis Inlet, which has an inner sill, the high turbidity layer is more prominent inside this sill than in the main basin. Since tidal currents would be expected to be smaller inside the inner sill than outside, this fact tends to support the turbidity current idea. Such currents starting at the head would be trapped, in part at least, by the inner sill.

Another feature which is unexplained is the irregular occurrence of high turbidity water in Calm Channel. The fact that this water is *not* isothermal or isohaline argues against intense vertical mixing. This region is believed to be approximately where the flood tides from north and south meet and it is possible that a particular water body might be held here relatively unchanged for some time. This is less likely to be the case further north or south where the tidal excursion is appreciable.

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THE TOXICITY OF *GONYAULAX MONILATA* HOWELL TO *MUGIL CEPHALUS*

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ABSTRACT

Laboratory experiments were conducted to determine the effects of *in vitro* cultures of the marine dinoflagellate, *Gonyaulax monilata* Howell, on fishes. Results indicate that the organism produced a substance(s) toxic to fishes and that the toxicity of the medium is increased if the dinoflagellate cytolyses.

INTRODUCTION

Connell and Cross (1950) reported the concurrent appearance of red, luminescent water, large numbers of a marine dinoflagellate, *Gonyaulax* sp., and the mass mortality of fishes in Offats Bayou near Galveston, Texas. They did not identify the species of *Gonyaulax*, but their report contains photographs and drawings of the associated, chain-forming organism. Howell (1953) reported the occurrence of red water, fish mortality and blooms of *Gonyaulax*, which he described as *Gonyaulax monilata*, in a location near Melborne, Florida. Gunter (1942) had previously reported yearly summer mortality of fishes in Offats Bayou during the period from 1936 to 1941 and, according to Connell and Cross, local residents had observed this red water and dead fishes almost every year during the 15–20 years prior to 1949.

During September 1955, we observed "red water" and dead fishes in Offats Bayou. The organism responsible for the water discoloration was *Gonyaulax monilata*. The samples we collected contained between 500 and 1000 organisms per ml. We were able to establish bacterized cultures of this species in the laboratory at that time. Subsequently, mass cultures of *G. monilata* were established and tests were conducted to determine the effects, if any, of the cultures on fishes.

The results of these tests indicate that bacterized cultures of *Gonyaulax monilata* are toxic to fishes and blooms of this organism may be the direct cause of associated fish mortality. The results of these tests were similar, in that the *Gonyaulax* culture was toxic to fishes and the uninoculated media were not. The experiments differed in the size, number and species of fish tested and the time required for the death of fishes to occur. The data from one experiment are presented in this paper.

METHODS AND MATERIALS

The materials used in this experiment consisted of 10 liters of artificial sea water medium (Table 1), 5 liters of which were placed in each of two Pyrex bottles (2½ gal). Both bottles were autoclaved at 15 lbs for 30 min. One of the bottles of medium was inoculated with 10.0 ml of a bacterized culture of *Gonyaulax monilata*. Both the inoculated and uninoculated bottles were placed adjacent to two 40 w, standard, cool white, fluorescent tubes.

After 3 months, at which time the test was conducted, the inoculated medium contained approximately 1,400 *G. monilata* per ml.

Aliquots of both the *G. monilata* culture and uninoculated medium were treated as follows: A) unaltered; B) heated to 50°C and allowed to return to room temperature; C) frozen for 24 hours, thawed, and allowed to return to room temperature; D) aerated throughout the experiment; E) millipore filtered with AA membrane (filtrate); F) millipore filtered culture (residue from E reconstituted in 600 ml of uninoculated medium). The residue of the filtered uninoculated medium was not used.

Young mullet (*Mugil cephalus*) were maintained in aerated sea water for four days prior to the test. For the test, we used 600 ml of each of the 11 test media in one

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TABLE 1. *Composition of artificial sea water medium for growth of bacterized cultures of* Gonyaulax monilata *Howell*

	Amount per Liter[1]
NaCl	24.0 g
KCl	0.6 g
$MgCl_2 \cdot 6H_2O$	4.5 g
$MgSO_4 \cdot 7H_2O$	6.0 g
$CaCl_2$	0.7 g
K_2HPO_4	10.0 mg
KNO_3	10.0 mg
Vitamin B_{12}	1.0 μg
Thiamine HCl	10.0 mg
Biotin	0.5 μg
Sulfides[2]	1.0 ml
Vitamin Mix 8[3]	0.1 ml
Metals T[4]	5.0 ml
Adenine Sulfate	1.0 mg
Tris (Hydroxymethyl) Aminomethane	0.1 g (pH 8.2)
(Ethylenedinitrilo) tetraacetic Acid Disodium Salt	10.0 mg

[1] Raise to one liter with distilled water.

[2] Sulfides: NH_4Cl 0.2 g., KH_2PO_4 0.1 g., $MgCl_2 \cdot 6H_2O$ 0.04 g., $NaHCO_3$ 0.2 g., $Na_2S \cdot 9H_2O$ 0.15 g. Raise to one liter with distilled water.

[3] Vitamin Mix 8: thiamine HCl 20 mg., biotin 50 μg., Vitamin B_{12} 5μg., folic acid 0.25 mg., para-aminobenzoic acid 1.0 mg., nicotinic acid 10 mg., thymine 80 mg., choline 50 mg., inositol 100 mg., putrescine 0.8 mg., riboflavin 0.5 mg., pyridoxine 4.0 mg., pyridoxamine 2.0 mg., orotic acid 26 mg. Raise to 100 ml. with distilled water. (From Provasoli, *et al.*, 1956.)

[4] Metals T

	mg. per 100 ml.
Fe (as $Fe_2(C_4H_4O_6)3$)	5.0
B (as H_3BO_3)	5.0
Se (as H_2SeO_3)	1.0
V (as NH_4VO_3)	0.5
Cr (as K_2CrO_4)	0.2
Mn (as $MnCl_2 \cdot 6H_2O$)	1.0
Ti (as TiO_2)	5.0
Si (as $Na_2SiO_3 \cdot 9H_2O$)	5.0
Zr (as $ZrOCl_2 \cdot 8H_2O$)	2.0
Ba (as $BaCl_2$)	1.0

Raise to 100 ml. with distilled water.

liter beakers. Each beaker received six fish (average standard length 19 mm.) and was covered with polyethlyene sheeting. These were placed adjacent to 40 w, standard, cool white, fluorescent tubes. The temperature, at the test site, varied from 70° to 74°F.

Samples from each container were taken for pH determinations before adding the fish and at 7 hours after the start of the experiment. Samples were taken from each container for salinity determination, at termination (24 hours after start) of the experiment and from the stock culture of *G. monilata* and uninoculated medium.

Toxicity was determined by the length of time required for the six *M. cephalus* to die. Each fish was removed from the test material immediately upon death, so that the medium would not become excessively fouled.

RESULTS

A summary of the results of this test is contained in Table 2. As shown in this table, the fish died in less than 4½ hours in all aliquots of the *G. monilata* culture, except the millipore filter residue reconstituted in uninoculated medium. None of the fish died in the uninoculated medium, regardless of its treatment, within the 24-hour test period.

G. monilata culture heated to 50°C appeared to be the most toxic. The average survival time was 45 min. The next most toxic test material was the frozen culture, in which the average survival time of the fish was 56 min. In the millipore filtrate aliquot of the culture, the average survival time was 2 hours and 19 min, and in the unaltered and aerated aliquots of the culture, it was 3 hours and 5 min and 3 hours and 19 min, respectively.

DISCUSSION

Results of this experiment, and the others we conducted, indicate that *Gonyaulax monilata* produces a substance(s) toxic to fishes. Disrupting the dinoflagellates by heating or freezing the cultures appeared to increase this toxicity. The mullet in both heated and frozen *G. monilata* cultures died within one hour, whereas in the untreated culture the first fish did not die until over two hours had elapsed. This would indicate that toxicity does not depend on the presence of living organisms. Similar results with *Gymnodinium breve* were found by Ray and Wilson (1957) and by Starr (1958) who reports that the toxicity of a living culture of *G. breve* is increased by physical and chemical procedures which effectively destroy the organism.

The results indicate that the toxicity of a millipore filtrate is greater than that of the untreated culture, but the residue reconstituted in uninoculated medium did not

TABLE 2. *Effects of bacterized culture of* Gonyaulax monilata *on* Mugil cephalus

Container number and medium	Distress[1] time	Death[2] time	pH[3] before	pH[4] after	Salinity[5]
AI Unaltered *G. monilata* culture	1:55 2:01 2:49 3:03 3:08 3:09	2:04 2:47 3:02 3:16 3:17 4:03	8.0	7.7	29.62
AII Unaltered Uninoculated medium	None[6]	None	7.6	6.7	29.46
BI *G. monilata* culture heated to 50° C., then returned to room temp.	0:31 0:36 0:41 0:41 0:41 0:42	0:36 0:41 0:43 0:45 0:48 0:58	7.9	7.7	27.73
BII Uninoculated medium heated to 50° C., then returned to room temp.	None	None	7.5	6.6	29.59
CI *G. monilata* culture frozen for 24 hours, thawed, then returned to room temp.	0:47 0:47 0:48 0:50 0:51 0:51	0:50 0:51 0:57 0:57 0:59 1:00	8.0	7.8	29.51
CII Uninoculated medium frozen for 24 hours, thawed, then returned to room temp.	None	None	7.5	6.6	29.53
DI Unaltered *G. monilata* culture aerated during experiment	2:15 2:15 2:51 2:57 3:12 3:22	2:34 2:34 2:58 3:20 4:05 4:25	8.0	7.6	29.64
DII Unaltered Uninoculated medium aerated during experiment	None	None	7.6	6.8	29.48
EI Millipore filtrate of *G. monilata* culture (with AA membrane)	1:22 1:34 1:51 2:09 2:44 3:04	1:27 1:42 1:55 2:20 3:09 3:24	7.8	7.8	29.69
EII Millipore filtrate of uninoculated medium (with AA membrane)	None	None	7.5	6.6	29.45
FI Residue of Millipore filtered *G. monilata* culture, in uninoculated medium	None	None	7.5	6.6	29.83

[1] Time (hr:min) required for fish to show first visible signs of imbalance.
[2] Time (hr:min) of cessation of opercular movement.
[3] pH taken before fish were added to test medium.
[4] pH taken seven hours after start of experiment.
[5] Salinity samples taken at termination of experiment (24 hrs. after start). Salinity of stock bottle of *G. monilata* culture—32.70. Salinity of stock bottle of Uninoculated medium—32.60.
[6] The notation "None" means that no distress or death occurred within 24 hours after the start of the test.

kill the fish. It is assumed that the organisms were broken up by the suction of millipore filtration allowing more of the toxic portion to pass through the membrane.

Connell and Cross (1950) found that the fishes in Offats Bayou usually died when the *Gonyaulax* bloom "submerged" and suggested that the decrease of oxygen, that accompanied their submergence, was a contributing factor to the fish mortality. Our results indicate that if the submergence was actually the decomposition of *Gonyaulax* cells, fish would die at that time because more toxin(s) would be released. The results of subjecting fish to aerated *G. monilata* cultures indicate that the lack of oxygen was not the cause of fish deaths in this experiment. Maximum death time of fish in the aerated culture was only 22 min longer than in the untreated culture. Ray and Wilson (1957) have eliminated oxygen deficiency as a possible reason for toxicity caused by *Gymnodinium breve.*

Shilo and Aschner (1953), working with *Prymnesium parvum* found that the toxicity of this organism was decreased by mild acidity, oxidizing agents, absorbents, and bacterial growth. McLaughlin (1956) likewise found that cultures of *P. parvum* grown in alkaline media were far more toxic

than if the pH was reduced, but subsequent raising of the pH restored toxicity. Further work is needed with *Gonyaulax monilata* concerning these factors that may influence toxicity.

Symptoms of human shellfish poisoning associated with blooms of *Gonyaulax catenella* and *Gonyaulax tamarensis* are primarily peripheral paralysis and death by respiratory failure (McFarren, *et al.* 1956). *Mugil cephalus* when exposed to *G. monilata* culture, first exhibits distress by frenzied activity, followed by the loss of equilibrium. The fish then turns upside down or on its side and shows slow opercular movements. It may remain in this position, either floating or lying on the bottom of the container, for some time. Immediately before death, there is a violent burst of activity and the fish dies with mouth and opercula open. Since *G. monilata* seems to have a paralyzing effect on mullet, it would be interesting to compare the effects of the toxin(s) produced by *G. catenella* and *G. tamarensis* with *G. monilata* toxin, on mice or other test animals.

Additional tests with bacteria-free cultures are needed to determine the contribution of bacteria to the toxicity of the cultures.

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TEMPERATURE, SALINITY, AND SOUTHERN LIMITS OF THREE SPECIES OF PACIFIC COTTID FISHES

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ABSTRACT

Three species of cottid fishes, *Oligocottus maculosus, Clinocottus globiceps,* and *Leptocottus armatus,* were subjected to tests to determine their relative degree of tolerance of elevated temperature and salinity. They were found tolerant of approximately double strength sea water for up to 14 hours, at 12°C. Elevation of temperature resulted in partial failure of osmoregulation at about 16°C in the first two named species and at about 25°C in *L. armatus.* The temperature related reaction to osmotic stress can be related to maximum shore temperatures at the southern extremity of the ranges of *O. maculosus* and *C. globiceps.* In intraspecific comparison, tolerance of elevated salinity does not imply tolerance of high temperature and *vice versa.*

INTRODUCTION

I am obliged to the National Science Foundation for financial support (Grant NSFG–4384) of this study.

Generally speaking, it is difficult to relate geographic ranges of marine fishes to a single limiting ecological factor. Ranges of many marine species conform to patterns that can be related to combinations of temperature and salinity, or other ecological variables. Cause and effect relationships in such distribution patterns have been difficult to define. Experimentally, using techniques that afford any sort of manageable data, one generally finds apparent tolerances comfortably outside those limits that the animals might encounter in nature. It has often been concluded that limits of natural ranges are the result of combinations of several factors, subtle in their expression, and elusive of definition. Pearse and Gunter (1957) and Gunter (1957) have recently discussed the subject.

The present study considers temperature and salinity as factors that possibly limit directly the southern extent of the vegetative ranges of three species of eastern Pacific fishes of the family, Cottidae, and the extent to which tolerances of the two stresses are related.

Approximately 10% of the species of marine fishes of the Pacific coast of the United States belong to the Cottidae. Most species of the family are small and many live in the intertidal zone. The family is generally considered to be a derivative of some fresh water serranid and is of recent, marine origin, stemming from the North Pacific (MacFarlane 1923). The family has spread southward in the seas and fresh waters of the Northern Hemisphere. Only one species, a deep water form, has been found south of the Equator (Bolin 1952).

The rather obvious relationship that the distributions of these fishes show to both temperature and salinity gradients makes certain of the species commendable subjects for experimental study of effects of these physical factors. Southern limits of the ranges of a number of the species are sharp and consistent, indicating that limiting factors should be reasonably well defined.

MATERIALS AND METHODS

The species considered in the present work are *Oligocottus maculosus, Clinocottus globiceps,* and *Leptocottus armatus.* Small specimens, from 20 to 35 mm in length, were taken to the laboratory and held in aerated sea water of approximately 21‰ and at approximately 12°C, subsequently referred to in this paper as the "conditioning point." It is not to be taken as any sort of acclimation treatment. It was used simply as a base to help unify test conditions. Such conditions are regularly encountered by all three species in nature.

The animals were held in conditioning jars for periods of from 12 to 144 hours prior to use in the tolerance tests. They were not

fed during their stay in the laboratory. Exploratory studies demonstrated that there was no measurable loss of viability during the first 6 days of laboratory life. Other tests, after conditioning at different levels of salinity and temperature for periods of up to 5 days, demonstrated that there was no measurable degree of acclimation resulting from such periods of preliminary treatment.

The tolerance tests were carried out in a water bath having a capacity of approximately 25 gal. Temperature was maintained by recirculating refrigerated water counteracted by an 850 w electric heater. The heater was controlled through a relay by a thermosensitive mercury switch. Constancy of temperature could be maintained within 0.1°C for extended periods. Bath conditions were kept uniform by a cone drive stirrer.

Sea water was taken to the laboratory in carboys and required salinities were established by evaporation or by dilution with fresh water. In the early experiments natural spring water was used to make necessary dilutions. It was found that tap water, rid of its heavy metals and chlorine residuum, gave the same results when used instead of spring water. The water was filtered through pyrex wool to free it of detritus. Salinity was determined by conversion from chlorinity by multiplying the latter by a factor of 1.8. Chlorinity was determined by titration following the method outlined by Harvey (1945). The sodium chloride standard used during the work was checked against *eau de mer normale* obtained from Kahl Scientific Corporation, El Cajon, California.

In the tolerance tests, the fishes were placed individually into 600 ml beakers containing 300 ml of water. The beakers were painted black to minimize visual stimulation that might result from activities in the laboratory or activities of the other fishes. The beakers were supported by a wire tray in the water bath. Aeration was by bubbling through glass air tubes at a rate adequate to maintain saturation but not vigorous enough to disturb the animals.

The fishes were placed directly into the test beakers from the conditioning jars. From 5 to 20, usually 10, fish were used in each test. Test conditions were maintained for 14 hours. If isolated in a tide pool, a fish would be relieved by at least one flood tide within this period. Mortality was recorded at the conclusion of the period.

During tests the beakers were kept constantly illuminated by a 100 w bulb placed over the center of the bath.

Conditions of these tests are admittedly arbitrary, however, they gave consistent, reproducible results and data that I believe are ecologically significant.

Approximately 2000 fishes were used in conducting the tests. No fish was used in more than one test.

NOTES ON THE BIOLOGY OF THE THREE SPECIES CONSIDERED

The ranges of all three of the species extend north along the coast of Alaska to the vicinity of 60°N. As to occurrence in any significant numbers, the southern limits of the ranges of *C. globiceps* and *O. maculosus* are found in the vicinity of San Francisco, California at about 37° 30′ N. South of that, *Clinocottus recalvus* replaces *C. globiceps*, and *Clinocottus analis* replaces *O. maculosus* in comparable habitats. *Leptocottus armatus* extends south to San Quintin Bay, Baja California, at about 30° 30′ N (Bolin 1944). As far south as San Diego Bay it appears to occupy a position in the community similar to that which it occupies 15° of latitude northward. In comparable habitats, what fishes replace it along the Baja coast I do not know.

TOLERANCES OBSERVED

Preliminary tests demonstrated that at a temperature of 12°C all three of these species would tolerate salinities of the order of double strength sea water for extended periods. (see Fig. 1.)

Leptocottus armatus was tolerant of a salinity of 67.5‰ at 12°C. Its tolerance of high salinity failed gradually with rising temperature up to about 25°C. At this temperature there was a precipitous fall in tolerance down to a salinity level of 37.5‰.

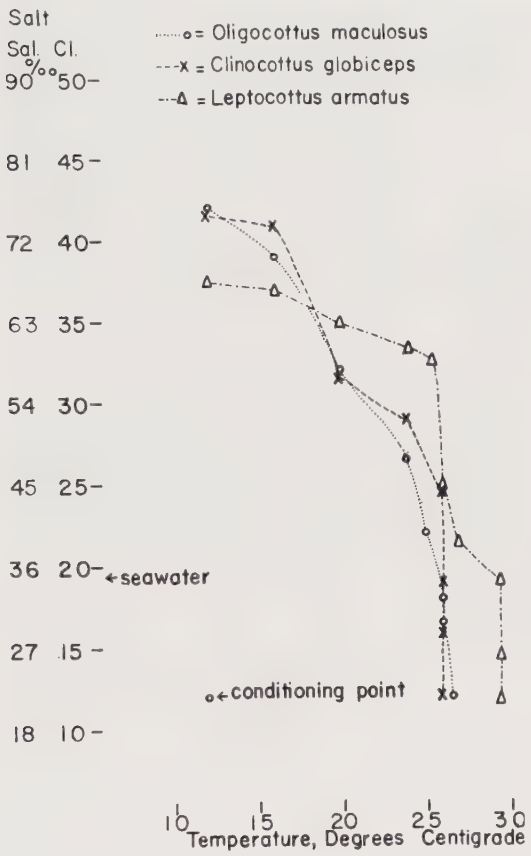

FIG. 1. Temperature and salinity tolerances of three species of cottid fishes. Temperature is indicated on the X axis, salinity on the Y. The points shown are those at which there was at least 50% survival of the test animals. Mortality exceeded 50% at levels within 2.0‰ chlorinity or 0.5°C. above the survival points shown.

Below a salinity level of 37.5‰ temperature tolerance was extended on to 29.5°C at a salinity of full strength sea water. Dilutions below this salinity level neither alleviated nor aggravated temperature tolerance, at least down to a level of 21.0‰.

Tolerances of *Clinocottus globiceps* and *Oligocottus maculosus* are similar both as to extremes and intervening breaks. At 12°C both species are tolerant of salinity levels of about 75‰. Tests run at 9°C indicate no further increase in salinity tolerance at temperatures lower than those shown in Figure 1. There is a drop in salinity tolerance at about 15°C, being most conspicuous in *C. globiceps*. A less pronounced diminution of salinity tolerance is observed as temperature is increased from 20 to 24°C. Further increase of temperature to 26.0°C reduced the salinity tolerance of *C. globiceps* to 44.0‰ and this was the maximum temperature at which this species could survive at any salinity level. Such temperature tolerance in *O. maculosus* is not reached until the salinity is lowered to that of sea water. This species can survive at 26.5°C when the salinity level is dropped to 21.5‰.

DISCUSSION

Osmoregulation in bony fishes has been the subject of a number of investigations involving several species of marine forms and the mechanisms have been extensively discussed (*e.g.* Smith 1930 and Forster 1953). Among the bony fishes there are no known mechanisms for regulation of temperature. It seems reasonable to treat osmoregulation as a function of temperature under conditions of the tests considered here. Although Kinne (1956) makes a case for distribution being dependent upon the compensatory and complementary effects of salinity and temperature, he does so largely on the basis of reactions of marine invertebrates that are found in estuaries and other dilute waters; perhaps in spite of the dilution, rather than because of it. At any rate, the water and salt problems that confront marine fishes are substantially different from the osmotic problems of marine invertebrates. Gunter (1956) describes a close correlation between distribution of several species of fishes and salinity patterns. Here again, an estuarine situation is considered. As a result of such findings regarding estuarine forms there has developed a rather prevalent inclination to weigh salinity heavily in assessment of factors directly affecting distribution of fishes in the sea.

Figure 1 indicates that the apparent osmoregulatory abilities of three cottids are substantially greater than the natural environment should ever demand in setting the limits of vegetative distribution of the juveniles. Since larval development of all three species is planktonic in open water, it would seem that salinity would not be

likely to limit reproductive distribution either. At 12°C the salinity tolerance of the three species is virtually inversely related to their southern spread. *Leptocottus armatus* is the least tolerant but has spread the farthest south in spite of its estuarine habitat. *L. armatus* juveniles show no increase in temperature tolerance in dilutions below full strength sea water. There seems to be no evidence that the direct influence of salinity has restricted its southern spread.

At or below the salinity of sea water those temperatures that result in death after 14 hours of exposure cannot be related to temperatures that obtain at or near the southern limits of the respective ranges. At sea water salinity, temperature tolerances of the three species do show a direct relationship to the limits of their respective southern distributions. These temperatures appear to be considerably higher than any that could conceivably be encountered in nature.

Figure 1 shows that in the temperature-salinity tolerance lines of all three species there are definite breaks at temperatures below those occurring at the maximum temperatures tolerated. A break in the tolerance line of *C. globiceps* is well defined at 16°C. A break is present but not as well defined near the same temperature in a line representing *O. maculosus*. In the line representing *L. armatus* there is a strong break between 25 and 26°C.

A break in the line at a temperature below the maximum tolerated indicates a sudden loss of efficiency either because of the direct adverse effect of increased temperature on one or more of the mechanisms involved in osmoregulation and/or because of a sudden increase in demand of one or more other metabolic processes. Coincidence of the position of the break in the line representing *Leptocottus* with the approximate maximum temperature tolerated by the other two species suggests that similar mechanisms are involved. The additional reserve of temperature tolerance in *Leptocottus* appears to be a special or additional physiological attribute. However, this is only a matter for speculation at the present time.

TABLE 1. *Abstract of daily shore temperatures (in degrees Centigrade) from Hopkins Marine Station, Pacific Grove, California. (From records compiled by Mr. Daniel M. Brown and Staff, Scripps Institution of Oceanography.)*

Year	Annual mean daily temperature	Maximum recorded during year	Number of days that the temperature exceeded 16°C.
1956	12.73	16.40	5
1957	13.74	15.70	43
1958	14.56	18.20	59

Although the maximum temperatures tolerated by these three species are unrealistic in terms of their natural environments, the breaks in the tolerance lines of *C. globiceps* and *O. maculosus* conform to temperatures encountered at the southern end of their ranges. Daily shore temperature records covering the past three years are shown in Table 1.

Hopkins Marine Station is located approximately 100 miles south of San Francisco at a latitude where *Clinocottus globiceps* and *Oligocottus maculosus* occur only occasionally. Temperatures during the warmest season of the year at this station are those at which the two species of fishes show marked loss of effectiveness as measured by osmoregulatory ability. Temperature records from the southernmost range of *Leptocottus* are not available.

SUMMARY

1. Using temperature tolerance as the criterion of salinity sensitivity there is no evidence that the three species considered in this work encounter salinity conditions in nature that could limit their southern distribution. One of the species, *Oligocottus maculosus*, demonstrates only a very slight increase in temperature tolerance with dilution below the salinity of full strength sea water; the other two species show none at all.

2. Using capacity for osmoregulation as a criterion of temperature sensitivity, all three species show definite reactions at temperature levels that they could reasonably encounter in nature.

3. Maximum shore temperature records from near the southern extremity of the

ranges of *Clinocottus globiceps* and *Oligocottus maculosus* are consistent with temperatures at which sensitivity was experimentally demonstrated. Comparable shore temperature records from the southern end of the range of *Leptocottus armatus* are not available.

4. In intraspecific comparison, tolerance of a high salinity level cannot be taken as indicative of tolerance of high temperature, and *vice versa*.

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COMPETITION BETWEEN *SIMOCEPHALUS VETULUS* AND *CYCLOPS VIRIDIS*[1]

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ABSTRACT

Simocephalus vetulus and *Cyclops viridis* were raised in pure and mixed cultures under controlled laboratory conditions. *Cyclops* numbers were depressed markedly in the presence of *Simocephalus,* whereas *Cyclops* had essentially no influence on numbers of *Simocephalus.*

Cladocerans and copepods are prominant among the zooplankton of freshwater lakes, and as such play an important role in trophic level dynamics. These animals are subject to extreme fluctuations in numbers and because of these have been the object of extensive study by limnologists.

Although the effects of certain environmental factors have been evaluated for some cladocerans, in particular *Daphnia,* relatively little effort has been concentrated on copepods. The relationship of daphnid cyclomorphosis to temperature has been studied by many investigators, among them Coker and Addlestone (1938), Kiang (1942), and Brooks (1946). Pratt (1943) has analyzed *Daphnia* population development at different temperatures; Ewers (1930), Coker (1933), and Aycock (1942) discussed the effect of temperature on species of *Cyclops.* Anderson *et al.* (1955) show that the number of cladocerans in

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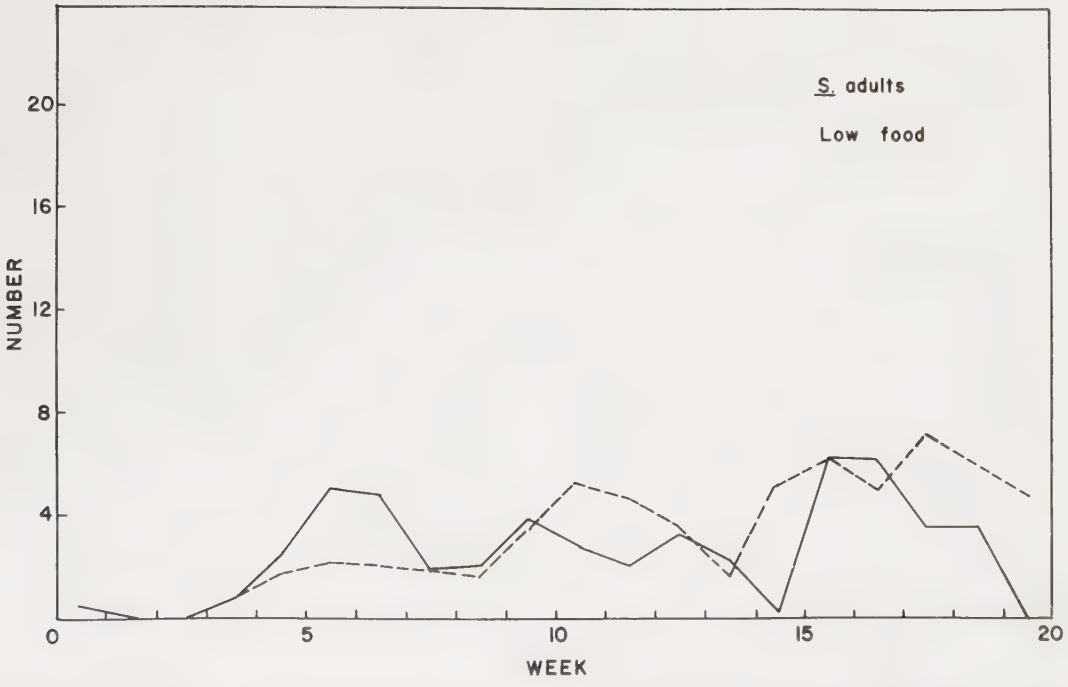

FIG. 1. Fluctuations in the progressive bi-weekly means of the numbers of *Simocephalus vetulus* adults in pure and mixed cultures at the low food level. (Solid line indicates pure cultures, dashed line indicates mixed cultures.)

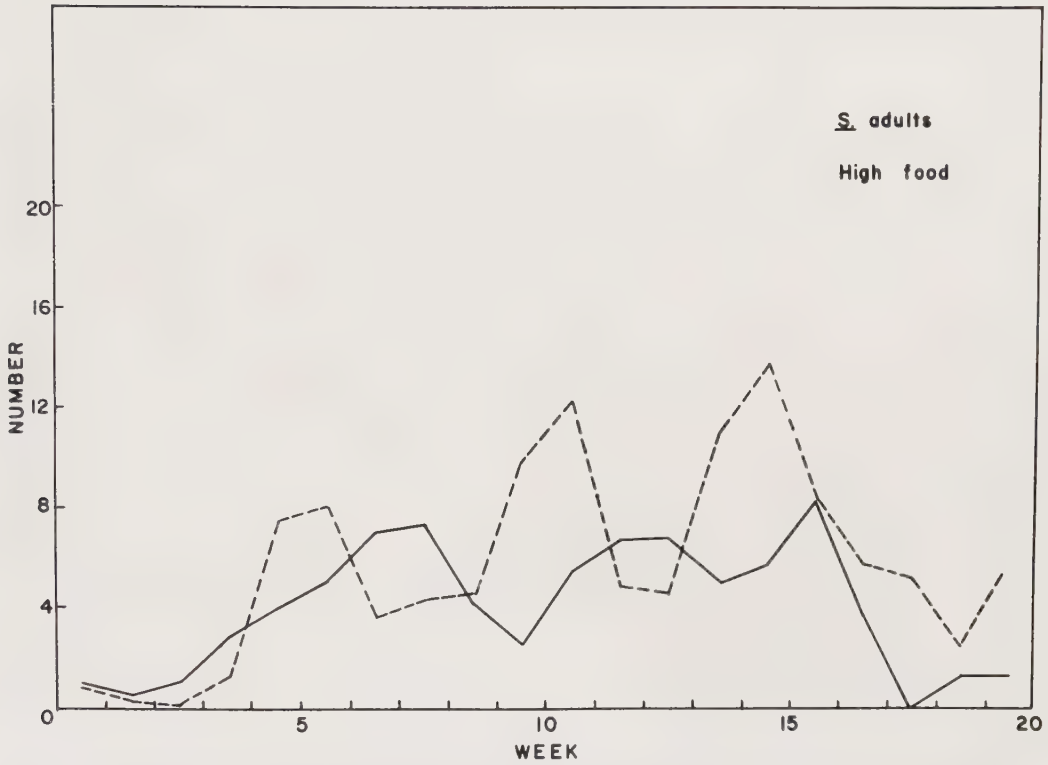

FIG. 2. Fluctuations in the progressive bi-weekly means of the numbers of *Simocephalus vetulus* adults in pure and mixed cultures at the high food level. (Solid line indicates pure cultures, dashed line indicates mixed cultures.)

Soap Lake, Washington, is not related to their winter phytoplankton food supply, whereas the number of copepods in Lake Lenore rises after the spring and fall phytoplankton maxima. These results may be atypical since both lakes are highly saline; also, Comita and Anderson (1959) have found that the *Diaptomus* population of Lake Washington is correlated positively with chlorophyll concentration. Ryther (1954) has shown that *Chlorella* will inhibit the growth and reproduction of *Daphnia;* however, Slobodkin (1954) found that the sizes of his *Daphnia* populations were directly related to the quantity of *Chlamydomonas* available as food. The latter is in support of work by Ingle, Wood, and Banta (1937) and Banta (1939).

Slobodkin and Richman (1956) studied the effects of removal of newborn *Daphnia* and concluded that the resulting increase in reproductive rate was due to the increased food supply for the remaining individuals. On the other hand, Frank (1952) found that when two cladocerans, *Daphnia* and *Simocephalus,* occupy the same medium, the former invariably eliminates the latter, and he concluded that direct density effects were operating.

Since cladoceran and copepod population peaks often fail to coincide, one is led to inquire into possible competition, either direct or indirect, which may act as a significant limiting factor. To evaluate this possibility, *Simocephalus vetulus* and *Cyclops viridis* (kindly identified by R. W. Kiser) were collected from Silver Lake near Spokane, Washington, to be raised under controlled laboratory conditions.

METHODS

In the spring of 1958, 320 cultures were started in small glass containers, each of which held 50 ml of Silver lake water fil-

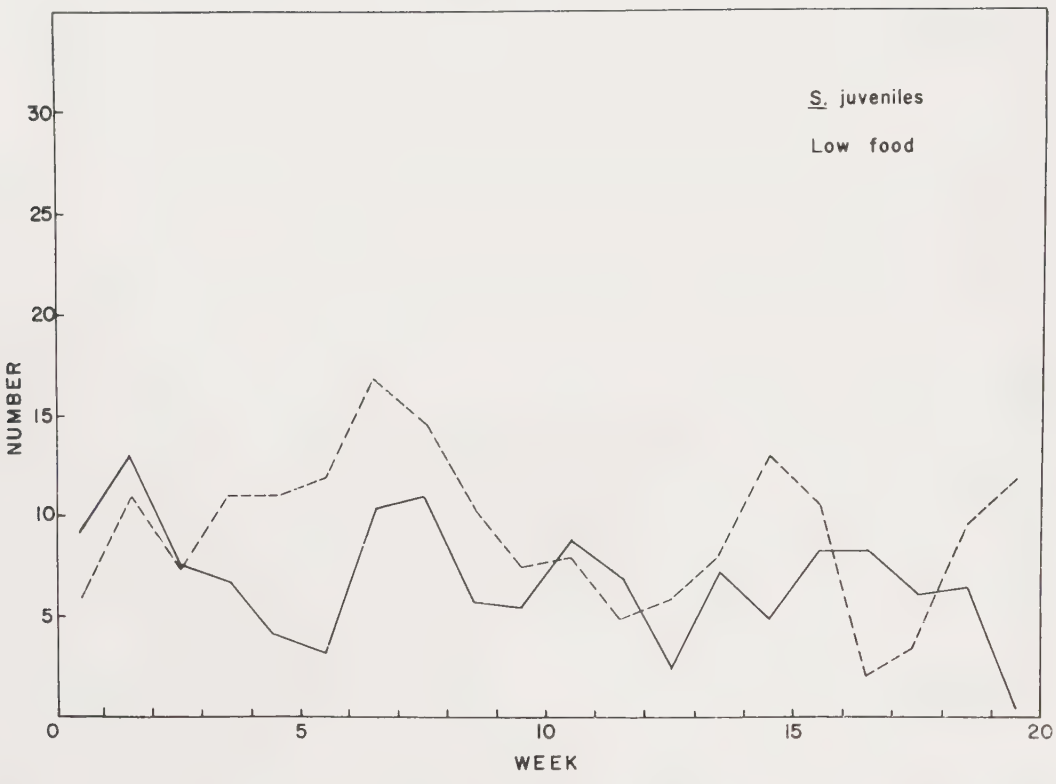

FIG. 3. Fluctuations in the progressive bi-weekly means of the numbers of *Simocephalus vetulus* juveniles in pure and mixed cultures at the low food level. (Solid line indicates pure cultures, dashed line indicates mixed cultures.)

tered through number 25 silk bolting cloth. The cultures were distributed as to content and number according to the following design:

	Simocephalus	*Cyclops*	*Simocephalus* × *Cyclops*
Low food	40	40	80
High food	40	40	80

More cultures were assigned to the mixed category because it was felt that the variability would be greater here. Each pure culture was initiated with one gravid female, whereas each mixed culture received one gravid female of each genus. All cultures were kept in a water bath at 20°C under continuous fluorescent lighting.

The animals were fed weekly with a suspension of *Chlamydomonas moewusii* having a Klett photometer density of 75 with a red filter. Those under low food received 1 ml and those under high food received 2 ml. The alga was raised in the following medium:

KNO_3	0.250 g
K_2HPO_4	0.100 g
$MgSo_4$: $7H_2O$	0.100 g
chelated iron	0.005 g
soil extract	167 ml
distilled water	833 ml

Sixteen cultures, two of each pure culture and four of the mixed cultures at each food level, were counted each week, and then were terminated due to the difficulty in making successful transfers of all *Cyclops* nauplii. Individuals were recorded in arbitrary classes. *Simocephalus*–juveniles and adults, and *Cyclops*–nauplii and copepodids (including adults). Although culture termination has rather obvious faults, it is apparent that this procedure results in

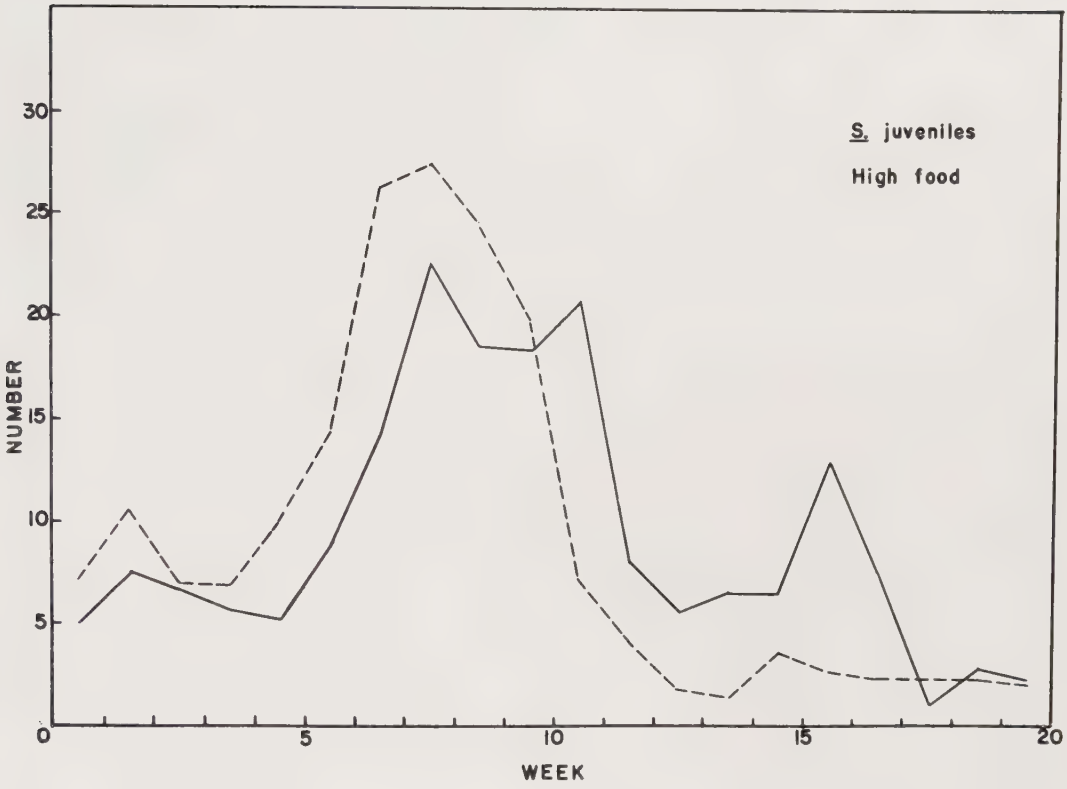

FIG. 4. Fluctuations in the progressive bi-weekly means of the numbers of *Simocephalus vetulus* juveniles in pure and mixed cultures at the high food level. (Solid line indicates pure cultures, dashed line indicates mixed cultures.)

independent weekly observations which lend themselves to reliable analysis.

RESULTS

Results are summarized graphically using progressive biweekly (two-week moving) averages of the mean culture sizes for each week. In these figures a maximum will be identified at any point where the slope is positive to the left of that point and negative to the right.

Simocephalus adults

At low food there appears to be little difference between the magnitude of fluctuations in numbers of adults in the two types of cultures (Fig. 1). In pure culture, maxima occur near weeks 5, 9, 12, and 15; whereas, in mixed cultures maxima occur near weeks 5, 10, 15, and 17. The mean times between maxima are 3.8 and 4.2 weeks, respectively, thereby suggesting that, if this difference is real, those animals grown with *Cyclops* develop at a slower rate.

When raised at the higher food level, the maxima are greater for the animals in mixed cultures and they occur somewhat in advance of those in pure cultures (Fig. 2); this is in contrast with the situation cited above. However, as will be shown later, a real difference between total population levels of pure and mixed cultures cannot be demonstrated.

Simocephalus juveniles

As was the case with the adults fed at the low food level, little difference between numbers of juveniles in pure and mixed populations can be noted (Fig. 3). Maxima are somewhat larger in the mixed cultures, and there are fewer of them.

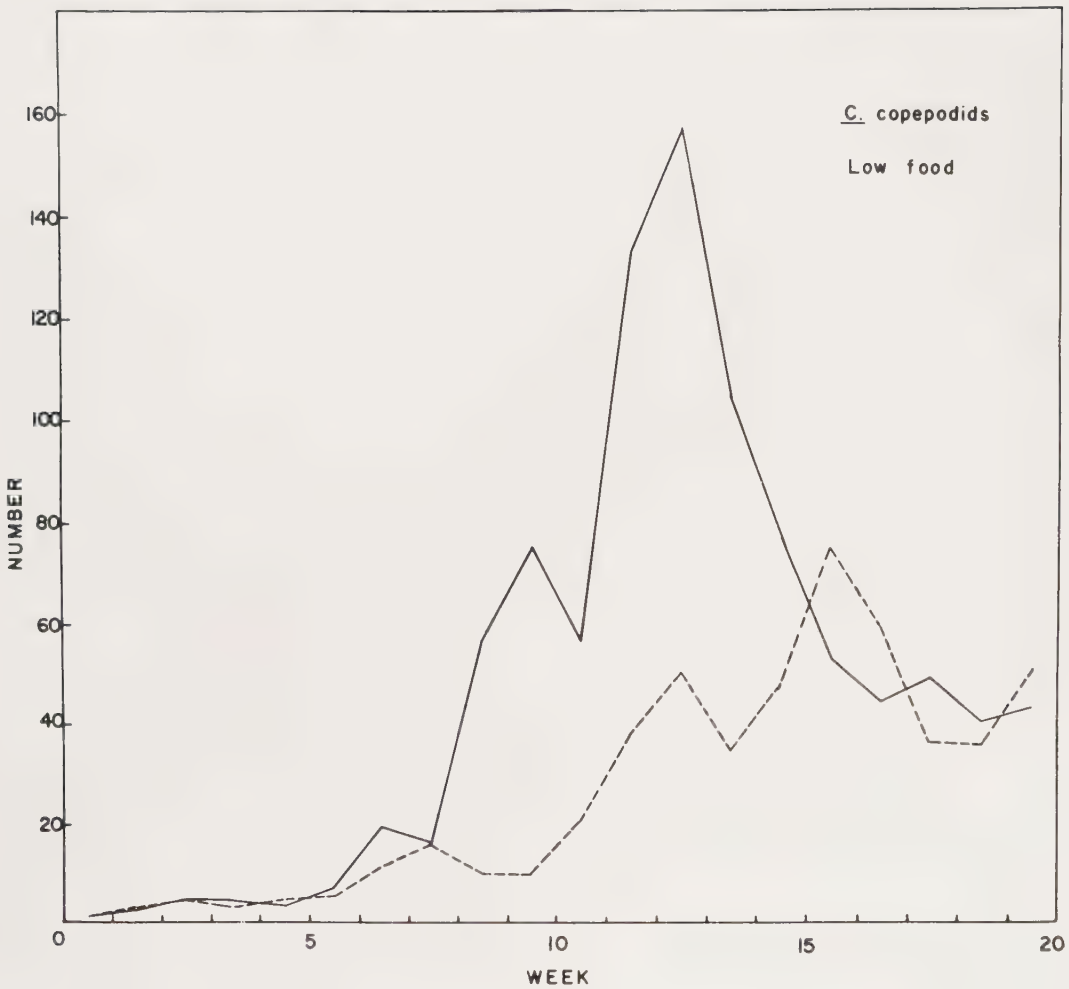

FIG. 5. Fluctuations in the progressive bi-weekly means of the numbers of *Cyclops viridis* copepodids in pure and mixed cultures at the low food level. (Solid line indicates pure cultures, dashed line indicates mixed cultures.)

When fed at the higher rate, isolated maxima were larger than for animals fed at the lower rate; however, it seems unlikely that there is any real difference between 20-week population means for either culture type (Fig. 4). As was noted for the adults at high food, the maxima in mixed cultures seemed to have occurred in advance of those in pure cultures.

Cyclops copepodids

Under conditions of low food, mean copepodid numbers in pure cultures reached a maximum of approximately 160 animals per culture: twice that of those in mixed cultures (Fig. 5). Furthermore, it is obvious that population development after three months in the pure cultures was about three weeks ahead of that in the mixed cultures.

At the high food level, differences between pure and mixed cultures are increased markedly; copepodids in pure cultures reaching 240 individuals and copepodids in mixed cultures reaching 80 individuals (Fig. 6). As above, there appears to be a lag in population development for those animals in mixed cultures.

TABLE 1. *Analysis of variance of total population size*

Source	*Simocephalus* d.f.	SS	MS	*Cyclops* d.f.	SS	MS
Culture type (C)	1	492	492	1	94429	94429***
Food level (F)	1	131	131	1	28169	28169*
Time (T)	19	5237	276	19	373579	19662
CF	1	245	245	1	258	258
CT	19	3033	160	19	167621	8822
FT	19	3578	188	19	73410	3864
CFT	19	2898	153	19	103660	5456
Residual	78	10705	137	80	346261	4328
Total	157	26319		159	1187387	

*** Significant at the 0.001 level.
* Significant at the 0.05 level.

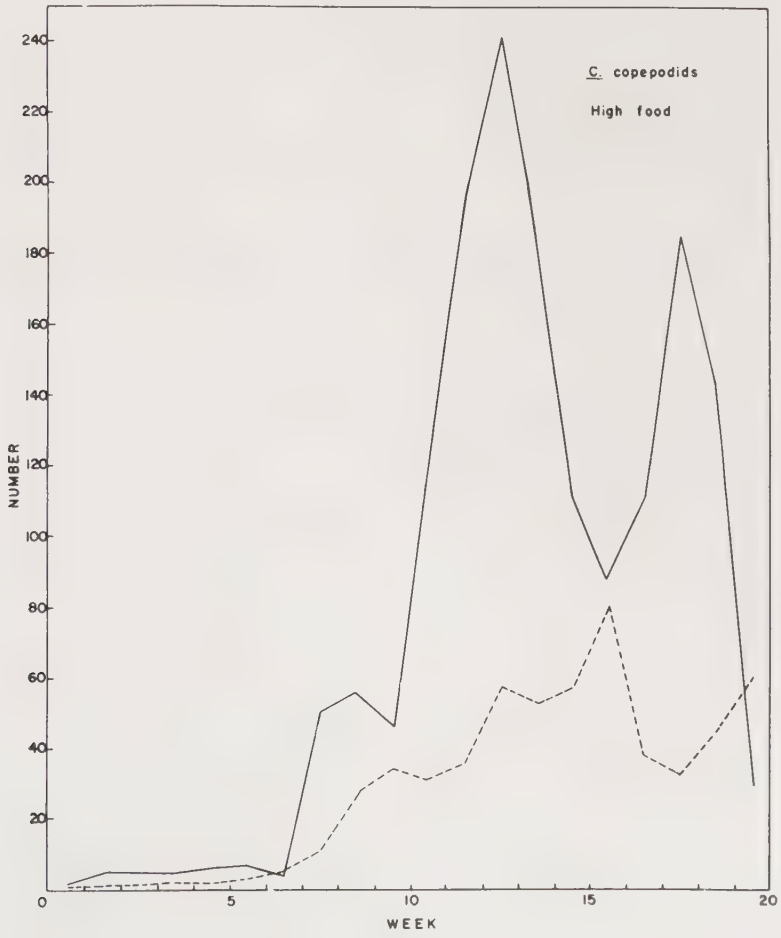

FIG. 6. Fluctuations in the progressive bi-weekly means of the numbers of *Cyclops viridis* copepodids in pure and mixed cultures at the high food level. (Solid line indicates pure cultures, dashed line indicates mixed cultures.)

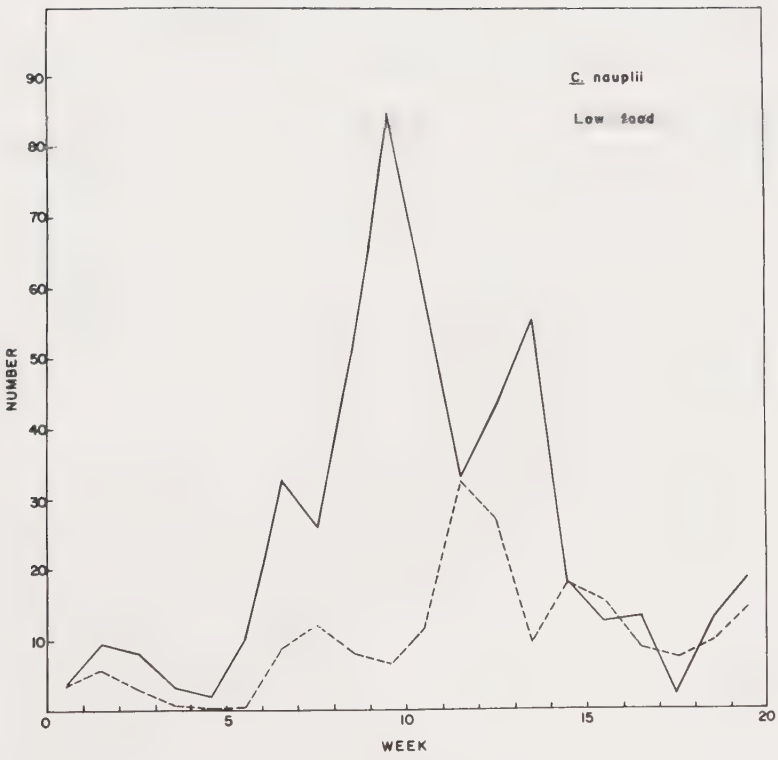

FIG. 7. Fluctuations in the progressive bi-weekly means of the numbers of *Cyclops viridis* nauplii in pure and mixed cultures at the low food level. (Solid line indicates pure cultures, dashed line indicates mixed cultures.)

Cyclops nauplii

When fed at the lower rate, numbers of nauplii reached 85 per container in pure cultures in contrast to approximately 30 in mixed cultures (Fig. 7). Again, the lag between culture types is evident.

A final comparison shows that nauplii fed at the higher food level reached maxima in pure cultures that were approximately twice that of those in mixed cultures (Fig. 8). Here the lag is not well defined.

The lag in population development of both *Cyclops* copepodids and adults grown in mixed cultures over those raised in pure cultures seems worthy of further comment. As was seen in the discussion of *Simocephalus*, there were instances of an apparently beneficial nature for those animals in mixed cultures. The opposite effect noted for *Cyclops* suggests that any benefit to the *Simocephalus* may have been at the expense of the *Cyclops* population.

Although graphical presentations are helpful in analyzing the results of these experiments, they are often misleading since the mean values used give no indication of the degree of sample variation. For those who prefer a more detailed account, an analysis of variance of total population size is given in Table 1. The 320 cultures were randomly divided into two groups, one for the analysis of *Simocephalus* populations and one for the analysis of *Cyclops* populations. Inadvertent loss of two cultures in the former group accounts for the difference in degrees of freedom. Here we see that there is a very highly significant difference between *Cyclops* population size in pure and mixed cultures, the former being much larger as seen in Figs. 5–8. The only other probable difference occurred between *Cyclops* populations raised at the two different food levels. In this case, there

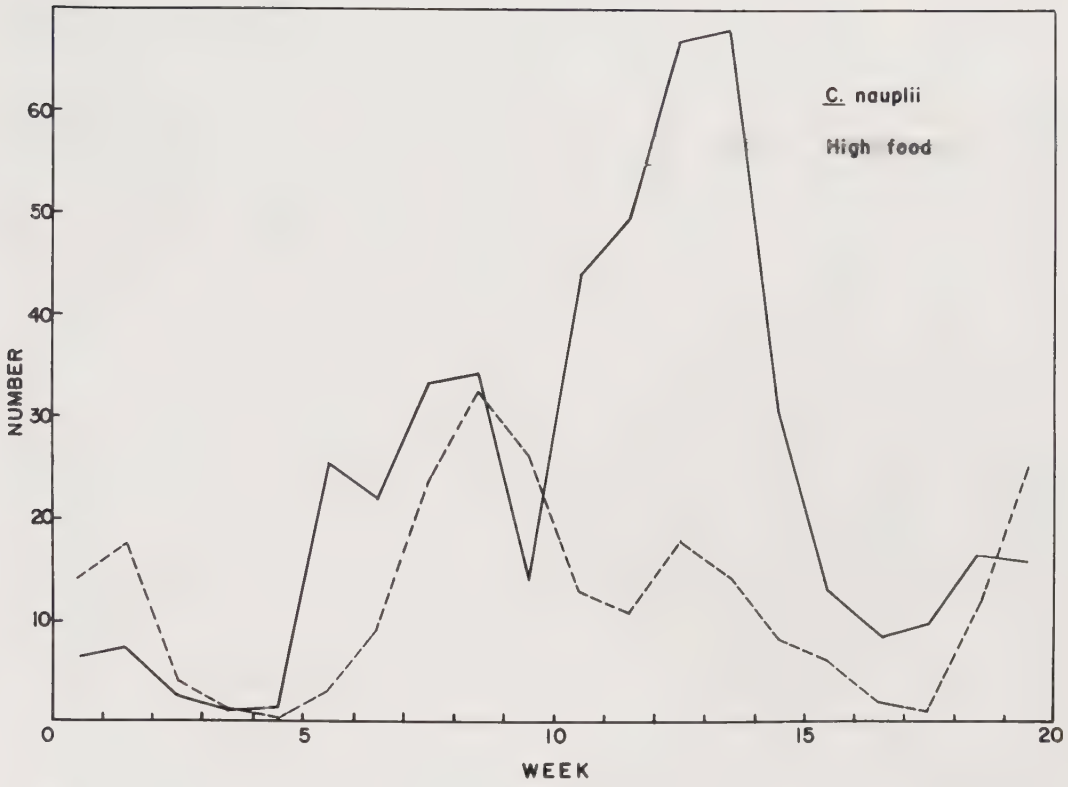

FIG. 8. Fluctuations in the progressive bi-weekly means of the numbers of *Cyclops viridis* nauplii in pure and mixed cultures at the high food level. (Solid line indicates pure cultures, dashed line indicates mixed cultures.)

were fewer animals when fed at the lower rate than at the higher rate.

DISCUSSION

It has been shown that joint occupancy by *Simocephalus* and *Cyclops* results in a depressed population of the latter. The cause of this depression is at this time unknown, however, one may speculate as to its nature.

Suspect is food supply although even at the low food level there always appeared to be a slight excess of the alga at the end of each week. It is possible, of course, that the presence of *Simocephalus* prevents proper feeding by *Cyclops* unless large quantities of food are available.

In order to make further discussion profitable, it is desirable to determine the part of the *Cyclops* life cycle affected. It is apparent that the cladoceran population must, in some way, partially inhibit successful reproduction of the copepod; however, detailed analyses of results from these rapidly fluctuating populations are extremely difficult. One may gain insight into the problem if numbers of *Simocephalus* can be correlated in some way with numbers of *Cyclops* nauplii. An approach which may yield the necessary information revolves around use of ρ, the rank correlation coefficient (Spearman 1906). This quantity behaves like the product-moment correlation coefficient in that it may vary between $+1$ and -1, with 0 indicating no relationship. For further discussion of this statistic the reader is referred to Kendall (1952). It is defined as

$$1 - \frac{6 \sum_{i=1}^{n} d_i^2}{n^3 - n}$$

where n is the number of paired observations and d_i is the difference between the

TABLE 2. *Analysis of lag effect by rank correlation of number of* Simocephalus vetulus *on number of* Cyclops viridis *nauplii at high food level*

	Number of paired observations									
Lag (weeks)	10	11	12	13	14	15	16	17	18	19	20
0	.39	.43	.31	.25	.13	.26	.31	.34	.39	.34	.28
1	.84	.80	.53	.49	.40	.47	.53	.55	.41	.30	
2	.67	.61	.56	.58	.52	.54	.56	.53	.32		
3	.67	.70	.64	.65	.55	.58	.46	.49			
4	.13	.14	.31	.39	.27	.40	.20				
5	−.27	−.18	.09	.20	.05	.17					
6	−.61	−.50	−.18	−.24	−.42						
7	−.63	−.52	−.54	−.57							
8	−.36	−.40	−.53								
9	−.57	−.55									
10	−.26										

ranks of members of the i^{th} pair. For example, consider five weeks of hypothetical population data for two species occupying a common habitat. Numbers of organisms are replaced by rank in the following table.

Week	Species 1	Species 2
1	1	1
2	3	5
3	5	4
4	4	2
5	2	3

Here $n = 5$, $\sum_{i=1}^{n} d_i^2 = 10$, and $\rho = 0.5$. If we had previously shown that species 1 was depressing species 2, we would of course be looking for a negative correlation. On this basis, we could simply realign the data and recompute ρ. To illustrate, let us look for a depressing lag effect by moving the species 2 data upward one week at a time. We might begin by using only data from weeks 1–3 for both species, then from weeks 1–3 for species 1 and 2–4 for species 2, and finally 1–3 for species 1 and 3–5 for species 2. Reranking the data for species 2 each time, we have:

No lag		1 week lag		2 weeks' lag	
Species 1	Species 2	Species 1	Species 2	Species 1	Species 2
1	1	1	3	1	3
2	3	2	2	2	1
3	2	3	1	3	2
$\rho = 0.5$		$\rho = -1.0$		$\rho = -0.5$	

Clearly the known detrimental effect of species 1 on species 2 is occurring maximally after a lag of one week. We might have begun with four weeks' data, thereby limiting our discovery of a lag effect to one week:

No lag		1 week lag	
Species 1	Species 2	Species 1	Species 2
1	1	1	4
2	4	2	3
4	3	4	1
3	2	3	2
$\rho = 0.4$		$\rho = -1.0$	

Again it is clear that the greater effect is taking place after a one week lag.

This technique has been applied to the number of *Simocephalus* individuals and the number of *Cyclops* nauplii in mixed cultures at the high food level (Table 2). For example, in the second horizontal line (one week's lag) the 10 paired observations comprise the averages of *Simocephalus* in weeks 1 to 10 compared with *Cyclops* in weeks 2 to 11; and that, at the extreme right, the 19 pairs are weeks 1–19 compared with 2–20, etc. Since autocorrelations have not been computed and the same data have been utilized to compute all of the ρ's, significance considerations are not justified; however, the pattern of the correlation values may prove useful. It suggests that a maximum positive correlation occurs around week three, whereas a maximum negative correlation does not occur until week seven. If this 7-week lag is real, it is obvious that the *Cyclops* depression is not due to the destruction of *Cyclops*' eggs by *Simocephalus*. Rather, it would seem that the *Simocephalus* interfere with the normal development of a group of *Cyclops* in such a way that their

future fecundity is reduced. The positive correlation needs to be explained.

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A QUANTITATIVE METHOD FOR THE COLLECTION AND MEASUREMENT OF STREAM PERIPHYTON[1]

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ABSTRACT

Two methods for the collection and estimation of stream periphyton production are presented.

The periphyton was collected on 1.4 dm^2 plexiglass plates attached to a horizontal crossbar. The crossbar was supported by a vertical post driven into the stream bottom or supported by a concrete block. The plates were removed from the stream and the established population estimated by determining the absorbency of the ethanol-soluble phytopigments and by gravimetric procedures.

A reliable estimate of the population can be made from the phytopigment absorbency values if the latter are corrected for deviations from the absorbency:concentration relationship and if the substrata are removed from the stream before the growth is too profuse. Confidence limits are given for the phytopigment density:weight of organic material relationship.

INTRODUCTION

Periphyton plays an important role in flowing waters because it is virtually the only primary producer in the ecosystem. Although this community is frequently subjected to adverse physical conditions such as high stream velocities or high turbidity levels, it is characterized by a very rapid recovery. Because of its ubiquitousness and rapid turn over it provides both food and shelter for the benthic fauna of a stream. Since the organisms involved are not equipped with a means of procuring the essential elements from the stream bed, the production of this community is also closely related to the characteristics of the water mass flowing by. Consequently, an evaluation of the periphyton community has long been recognized as a means of evaluating stream biodynamics.

When the periphyton of a stream is collected from the natural submerged objects, large variability results from difference in the texture and nature of the substratum. Because of this many workers have turned to the use of artificial substrata. Cooke (1956) gives a comprehensive review of the literature on the subject. The collected organisms are usually identified *in situ* and the characteristics of the community evaluated. Hooper, Ball and Hayne (ms) were the first to estimate periphyton production by using artificial substrata and the phytopigment extract method (Kreps and Verjbinskaya 1930, Harvey 1934, Manning and Juday 1941).

The methods described in this paper were used in an ecological study of the Red Cedar River, a productive warm-water stream which drains the south-central portion of the Lower Peninsula of Michigan. The stream is characterized by long pools or runs rarely exceeding four feet in depth which are separated by short riffle areas. The study was carried out by the authors over a 13-month period which included drought conditions, floods, and winter conditions when the stream was covered with as much as 12 inches of ice and 6 inches of snow. Qualitatively, the periphyton of the Red Cedar River consisted primarily of members of the Bacillariaceae. The dominant genera in the community varied with the season.

METHODS

The substrata used for the collection of periphyton consisted of plexiglass plates, 7

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FIG. 1. Plexiglass substrata and supporting devices used for the collection of stream periphyton.

mm in thickness, having an exposed area of 1.4 dm^2 when attached to a horizontal crossbar. The crossbar was either bolted to a steel post which was driven into the stream bottom or supported from a vertical upright which was wedged into a concrete building block (Fig. 1). The exposure depth was maintained with relation to the water surface in order to compare the production potential of several areas of the stream.

The plexiglass substrata were recovered after the periphyton mat was plainly visible, but before the growth was dense enough to slough off the surface of the plate. The exposure periods ranged from one to three weeks depending upon the accrual rate of the periphyton.

The substrata were removed from the stream, placed in individual plastic bags, and then frozen to aid in the release of the growth from the plastic. This procedure also facilitated the extraction of phytopigments by rupturing the plant cells.

Two methods of laboratory treatment were used: the first, a method designed to use phytopigment density *per se* as an index of periphyton production; the second, designed to investigate the relationship between phytopigment absorbency and organic weight.

In the first method the periphyton growth was scraped from the substrata and allowed to stand in 95% ethanol for a minimum of 48 hours in total darkness. It was found that samples could be stored in this manner for as long as 30 days without a loss of phytopigments due to decomposition. The samples were filtered through glass wool and the volume of the filtrate adjusted to 50 ml by either dilution or evaporation. The density of the phytopigment solution was read on a Klett-Summerson colorimeter (4

cm solution depth) using the red filter (640–700 mμ).

In the second method, all of the macrofaunal components were first taken from the substrate. The periphyton was then removed by scraping and washing with 95% ethanol. The particulate matter was then separated from the solvent by filtration through a Gooch crucible. The crucible was dried to constant weight and the organic components determined by loss on ignition. The absorbency of the ethanol-soluble pigments was determined after the solution was diluted to a volume of 50 ml. The solvent was then evaporated from the sample and the weight of the organic residue determined by loss on ignition. The weight of the residue was then added to the weight of the particulate fraction of the sample to give an estimate of total organic weight.

When two consecutive readings of ± 0.5 mg were obtained after an interval of 12 hours, the sample was said to be at constant weight.

RESULTS

Experiments showed that the absorption of broad spectrum light (640–700 mμ) is not linearly related to the concentration of 95% ethanol extracts of phytopigment except at very low concentrations. The deviation from the Lambert-Beer Law becomes apparent at an absorbency of 0.20 when read on a Klett-Summerson colorimeter and increases proportionately with higher concentrations. Nonlinearity was also noted for measurements made with monochromatic light at the peak absorption wavelength. Inorganic solutions (Harvey Standards) having comparable absorbencies did not exhibit nonlinearity with either monochromatic or polychromatic light. Therefore, it is believed this effect may be due to interaction between the solvent and solute or to changes among the molecules.

The measured pigment absorbency may be corrected to correspond with the theoretical absorbency as related to concentration by constructing a correction graph (Fig. 2). This graph is made by plotting absorbency against concentration as determined by dilution. This portion of the curve corresponds to the line labeled experimental in Figure 2. The line labeled Lambert-Beer corresponds to the theoretical absorbency of the solution.

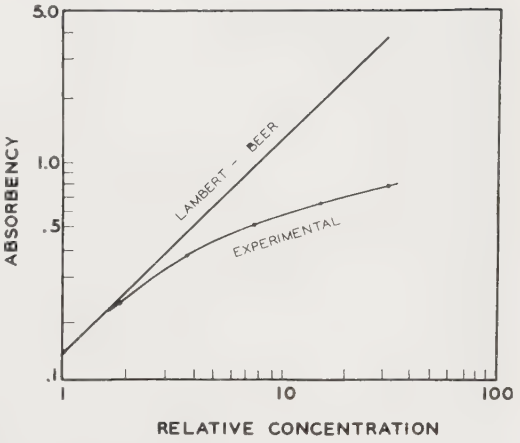

FIG. 2. A correction graph for adjusting measured phytopigment absorbency values to units related to concentration.

The correction graph is used in the following manner. The measured absorbency is found on the ordinate and is followed horizontally to intercept with the experimentally determined line; this intercept is then read vertically to intercept the extrapolated Lambert-Beer line; the absorbency unit on the ordinate opposite this intercept represents the corrected absorbency reading.

In order to avoid confusion between measured absorbency and corrected absorbency, the corrected absorbency will henceforth be designated as phytopigment units.

Experiments concerning the relationship between phytopigment units and organic weight showed that phytopigment units could be used to make quantitative estimates of organic weight when the value was less than 1.3 (Fig. 3). For samples having larger values the variations were too large to be useful as a quantitative technique. However, such samples are still valuable for comparative purposes.

It is believed that the increasing variation was due to the physical state of the algal

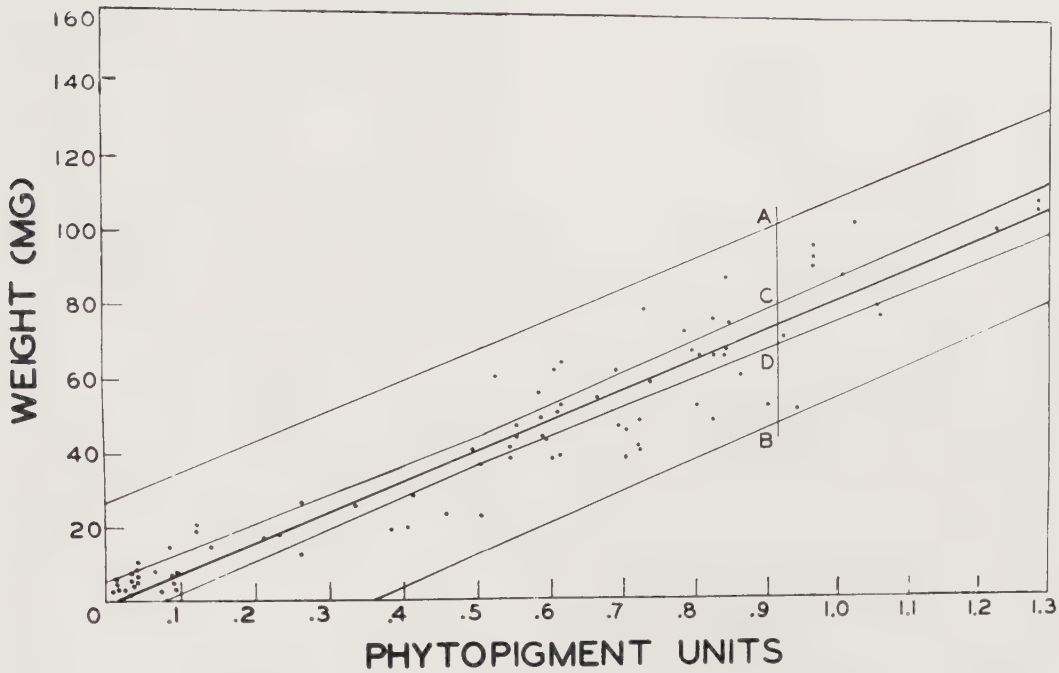

FIG. 3. The relationship between phytopigment units and periphyton weight. The 95% confidence regions are shown for estimates of $\hat{Y}$ (CD) and Y (AB).

colony. More specifically, the samples having the greatest variations were those which supported the most luxuriant growth of periphyton. Therefore, the increased variation is probably a combined effect of the death of some of the members of the colony and the accumulation of organic detritus on the surface of the substrate. For quantitative studies it is therefore important that the exposure period be short enough to avoid this condition.

The data presented in Figure 3 were collected from exposure periods ranging from one to three weeks depending upon the accrual rate of periphyton.

A linear regression was fitted to the phytopigment unit–weight relationship for values less than 1.3 (Fig. 3). The model used was Model 1 as given by Snedecor (1956). The sample regression equation for this model is

$$\hat{Y} = a + b\,X$$

where in this case

$\hat{Y}$ is the mean weight estimate
a is the intercept on the Y axis
b is the point estimator of the population slope
X is the observed phytopigment reading.

Using the computed constants the equation for predicting $\hat{Y}$ from X becomes

$$\hat{Y} = -1.72 + 82.37\,X.$$

Equations for computing a confidence region on the regression are given by Snedecor (op. cit.). The confidence region appears as curved borders on both sides of the regression. The width of the confidence region for any prediction made by X is dependent upon how far removed X is from $\bar{X}$ (the mean of the X's). Since all of the values of X in Figure 3 are near to $\bar{X}$ (0.518), the confidence region appears as two lines that are nearly parallel.

In Figure 3 a 95% confidence region is shown for estimates of Y (individual weights) and $\hat{Y}$ (mean weights). The maximum 95% confidence limit for any estimate Y made from phytopigment values ranging between 0 – 1.3 is ± 29.03 mg.

The minimum limit for any estimate of Y is found at $\bar{X}$, and in this particular case it is ± 28.43 mg. Similarly, the minimum limit on any estimate of $\hat{Y}$ is ± 3.05 mg and the maximum limit, ± 6.82 mg.

DISCUSSION

The two methods described for the collection and measurement of stream periphyton represent variations or adaptations of procedures utilized by other workers along with a statistical treatment of experimental data to relate the association between phytopigment density and the weight of organic material present on the collecting devices. The phytopigment density method represents a rapid technique utilizing relatively inexpensive laboratory equipment for the evaluation of periphyton production. This procedure may be used to determine the effects of organic enrichment on the periphyton community of a stream (Brehmer 1958) or to compare the production of areas within a stream system or to compare streams.

The relationship between the phytopigment density and the weight of organic material can be established to enable the investigator to place confidence limits on the data or to express the stream periphyton production in terms of grams/day/unit of surface area. In a stream where there are striking seasonal differences in the taxa of the periphyton community it might be desirable to compute a separate regression for each season. However, in this study one regression was found to be sufficient to make year-round predictions within the cited limits.

The method of collection can be used to study nutrient uptake by stream periphyton and has the advantage of providing the investigator with a sample of known state which is easily processed in the laboratory (Grzenda, Unpublished Report)[3].

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A LIMNOLOGICAL COMPARISON OF TWELVE LARGE LAKES IN NORTHERN SASKATCHEWAN

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ABSTRACT

Five large lakes on the rocky Precambrian Shield of northern Saskatchewan are definitely oligotrophic. Five others on the glacial drift south of the Shield are clearly eutrophic and two across the boundary are intermediate. From the analysis of extensive data, five physical and three biological criteria have been selected which tend to agree in indicating the trophic nature and relative productivity of these lakes.

INTRODUCTION

Limnological investigations of the lakes of northern Saskatchewan were begun by the writer nearly thirty years ago and have continued somewhat irregularly since that time. During the past ten years a continuous program has been aimed primarily at the provision of information needed for the effective management of game and commercial fisheries in the more important lakes. Much new data of basic limnological interest has resulted from this program. It is now appropriate that all the available information should be examined to see what generalizations can be reached as a first contribution to the regional limnology of the area. At the same time the various measurements will be examined critically to assess their utility in classifying this group of lakes, especially with regard to potential fish production.

The extensive data to be used in this analysis are the results of about fifteen summers' work, on twelve lakes, usually by field parties of three men. Thus, they can be treated only in summary and frequent reference will be made to information already published. The chief paper on Waskesiu Lake was published by the writer in 1935, one on Athabaska in 1947 and one on Lac la Ronge by Rawson and Atton in 1953. The five lakes of the Upper Churchill drainage were described by the writer in 1957, and the account of Cree and Wollaston lakes was published in 1959. Certain additional information concerning Lac la Ronge is contained in unpublished theses and in manuscript reports. The studies of Waskesiu and Lac la Ronge extended over several years and included some winter observations. Those of the other lakes, except Frobisher, continued through at least one full summer. While only twelve lakes are mentioned above, Hunter Bay which is connected to Lac la Ronge by a narrow channel, is considered sufficiently different from the main lake to warrant its treatment as a separate body of water.

Many persons have taken part in field work on the twelve lakes under consideration, and much credit is due to their enthusiasm and careful observations. Provincial Government administrators and field officers have given continued and generous assistance. Financial support for the work on Waskesiu Lake was provided by the University of Saskatchewan and for Lake Athabaska by the Fisheries Research Board of Canada. During the past ten years the field work has been generously supported by the Fisheries Branch, Saskatchewan Department of Natural Resources.

PHYSIOGRAPHY OF NORTHERN SASKATCHEWAN

The present fauna and the productive capacities of our lakes are, to a large extent, the result of their geological history, the development of soil and vegetation and the present climate of the area. Thus, in preparation for comparison of conditions within the lakes it is necessary to indicate the main physiographic features of the region. The area under consideration is the northern half of Saskatchewan shown in the location map (Fig. 1). It is about 500 km (310 miles) from east to west and

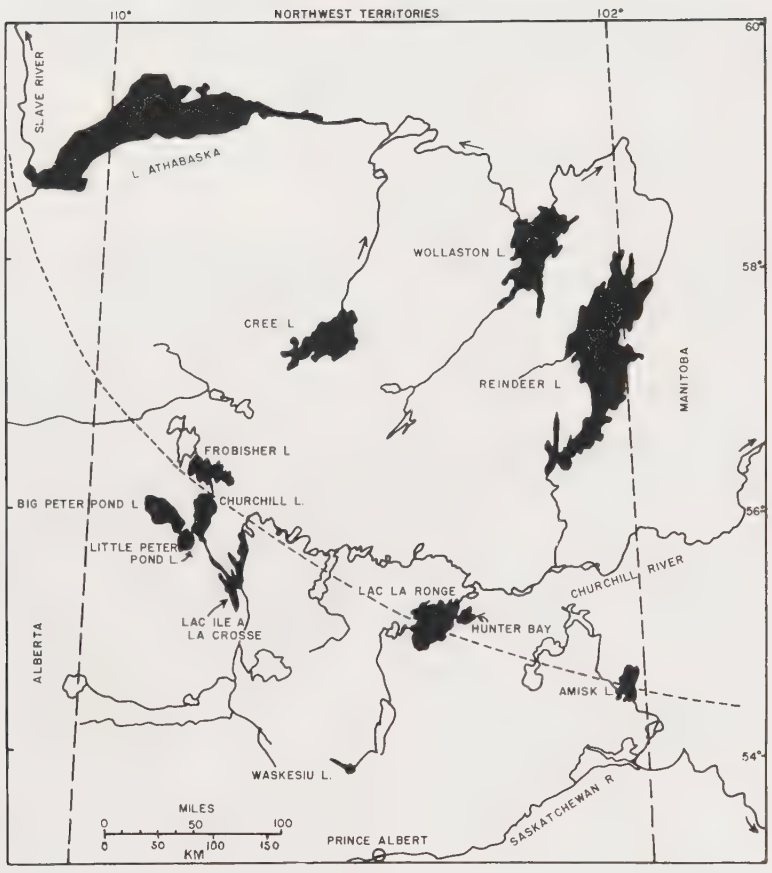

FIG. 1. Location of twelve lakes in northern Saskatchewan. The broken line indicates the southern margin of the Precambrian Shield.

more than 650 km (405 miles) from north to south. It contains about 4,000 named lakes and several thousand smaller ones, as yet unnamed.

The dominant feature of the geology of northern Saskatchewan is the Precambrian (Canadian) Shield which occupies most of the region (Fig. 1). It will be shown that the most significant feature of the twelve lakes under discussion is their location on the Shield, across its margin, or on the glacial drift to the south of this margin. The Shield generally is thought of as a great area of low or moderate relief with exposed granite ridges and sparse vegetation. This would apply to much of the area around Wollaston and Reindeer lakes which is of Archaean (early Precambrian) age. Cree Lake, however, lies on the southern part of the great area of Athabaska Sandstone, of late Proterozoic age. Thus, Cree Lake is marked by innumerable sandy beaches and high sand cutbanks. Nearly one-third of the numerous islands in Cree Lake are drumlins (Sproule 1939). The sand-covered region extends far to the northwest and forms the south shore of Lake Athabaska. Frobisher Lake lies on the south part of the Shield, but the remaining four of the Upper Churchill group lie in basins of glacial drift, underlain by sedimentary rocks of Devonian age. Lac la Ronge and Amisk lie across the margin of the Shield, but their geological surroundings are not entirely comparable. The north half of Amisk is on the Precambrian and the south on dolomites and sandstones of the Upper Ordovician. Thus, it is surrounded by rocks

and receives its drainage from rocky territory. Lac la Ronge has it north half on the Precambrian but its southern part is on glacial drift, and it receives most of its inflow from soil-covered areas to the south. Waskesiu is much further south on deep glacial drift underlain by strata of Cretaceous age. Some additional comments on the geological surroundings of the lakes are included in the five papers referred to in the introduction. For further information on the geology of the region, the reader is referred to Stockwell (1957).

The lakes of northern Saskatchewan drain into three great river systems. Cree Lake and Athabaska drain northwest through the Athabaska-Mackenzie system to the Arctic. Wollaston Lake is unusual in having two major outlets. A part of its outflow goes through the Fond-du-Lac River to the Athabaska and a somewhat larger amount through the Cochrane River to Reindeer Lake and thence into the Churchill system. Most of the lakes under consideration drain eastward through the Churchill River. These include the five so-called Upper Churchill Lakes, Lac la Ronge and Waskesiu. Waskesiu lies far south of the Churchill River at an altitude of 531 m (1740 ft) and close to the height of land between the Churchill and Saskatchewan drainage areas. Amisk Lake, in the southeast part of the area, drains south into the Saskatchewan River and thence east toward Hudson Bay. Cree Lake with an altitude of 479 m (1570 ft) is the highest of the lakes on or near the Shield and has a relatively small drainage area. Athabaska at the northwest has an altitude of 213 m (699 ft), the lowest of any lake in the province.

The climate of northern Saskatchewan might be described as typical of continental taiga, with long cold winters, low precipitation and low moisture requirements for its vegetation. The most useful observations are from three stations, Fond-du-Lac at the east end of Lake Athabaska, La Ronge near the south edge of the area, and Island Falls on the Churchill River about midway between Amisk and Reindeer lakes (Boughner and Thomas 1948; Kendrew and Currie 1955). The isotherms tend to cut across the area from northwest to southeast. Thus the warmest part is to the southwest and the coldest at the northeast corner of the province. In the center of the area the mean air temperature in July is about 16.6°C (62°F) and in January –24.4°C (–12°F). The annual precipitation is about 40.6 cm (16 in), of which nearly one-third falls as snow. Since the rates of evaporation and transpiration are moderate in this area, there is little moisture deficiency and the climate would be classified by Thornthwaite (1948) as mainly dry subhumid but tending toward moist subhumid in the northeast. No permafrost has been reported near the lakes but it is said to occur along the Northwest Territories boundary north of Wollaston Lake. The ice cover usually forms on the southern lakes about November 20 and breaks up about May 15. In northern lakes, such as Wollaston, it forms about November 1 and remains until about June 15. Thus, the southern lakes have nearly six months of open water and a growing season at least six weeks longer than those in the north.

Northern Saskatchewan lies within the Boreal Forest Region as defined by Halliday (1937). This is a broad zone of mainly coniferous forest, characterized by white and black spruce but varying considerably according to differences in soil, drainage, temperature and humidity. Within this zone there is a marked gradation from a heavy proportion of deciduous trees at the south, through dense coniferous forest, to the thin subarctic woodland at the north. Some four or five sections may be distinguished. Thus Waskesiu lies in the center of the Mixed-wood Section where aspen and white birch are found with white spruce and other conifers. Churchill Lake, the Peter Pond Lakes and Ile a la Crosse lie in the Hyper-Churchill Section, a low area formerly occupied by a glacial lake. Here the forest includes much jack pine on the sandy areas and black spruce and tamarack in the swampy areas. Frobisher, La Ronge and Amisk lie in the Northern Coniferous Section with much jack pine, black and white spruce. Similar forest cover is found around Cree Lake and in the great sandy

TABLE 1. *Morphometric data for lakes in northern Saskatchewan*

	Athabaska	Cree	Wollaston	Reindeer	Frobisher	La Ronge	Hunter Bay	Amisk	Churchill	Big Peter Pond	Little Peter Pond	Ile a la Crosse	Waskesiu
Water area, km^2 (mi^2)	7,900 (3,050)	1,152 (446)	2,062 (796)	5,569 (2,150)	313 (121)	1,178 (455)	129 (50)	321 (124)	433 (167)	552 (213)	189 (73)	446 (172)	70 (27)
Mean depth, m	26.0	14.9	20.6	17±	5.5	12.7	20.7	13.2	9.0	13.7	5.1	8.2	11.1
Maximum depth, m	120	60	97	215	19	38	42	40	21	24	9.5	27	24
Shore length, km (mi)	1,900 (1,180)	786 (488)	1,475 (916)	2,370 (1,470)	424 (263)	830 (515)	185 (115)	195 (121)	212 (132)	124 (77)	63 (39)	570 (353)	76 (47)
Shore length of islands, km (mi)	248 (154)	845 (525)	1,410 (874)	2,000 (1,240)	362 (225)	950 (590)	82 (51)	150 (93)	89 (55)	0 (0)	8.9 (5.5)	47 (29)	.97 (0.6)
Shore development	6.0	6.5	7.5	9.0	6.7	6.8	4.8	3.1	2.9	1.5	1.3	7.6	2.6
Shore development with islands	6.8	13.6	14.7	16.5	12.5	11.6	6.9	5.4	4.1	1.5	1.5	8.2	2.6
Number of islands	633	546	370	2,500	697	1,160	145	488	56	0	8	59	1
Area of islands, km^2 (mi^2)	114 (44)	249 (96)	513 (198)	961 (371)	119 (46)	114 (44)	13 (5)	91 (35)	19.4 (7.5)	0 (0)	1.04 (0.4)	6.0 (2.3)	.08 (.03)
Islands % total area	1.4	17.7	19.9	14.5	27.5	8.8	9.1	22.0	4.3	0	0.5	1.3	0.1
Altitude, m (ft)	213 (699)	479 (1,570)	397 (1,300)	351 (1,150)	422 (1,384)	366 (1,198)	366 (1,198)	294 (964)	422 (1,383)	422 (1,383)	422 (1,383)	421 (1,382)	531 (1,740)
Drainage area, km^2 (mi^2)	— —	4,467 (1,725)	23,310 (9,000)	64,750 (25,000)	4,921 (1,900)	14,763 (5,700)	259 (100)	13,468 (5,200)	7,874 (3,040)	9,713 (3,750)	13,105 (5,060)	77,700 (30,000)	1,114 (430)
Period of "flushing," years	—	—	14	11	—	19	—	3	10	12.5	1.6	0.75	—

area extending northwest to the south shore of Lake Athabaska. The extreme north of the province lies in the Northern Transition Section, essentially equivalent to the taiga of other classifications, where the Boreal Forest thins out and eventually grades into the Tundra. This section borders the north shore of Lake Athabaska, and farther east its boundary dips south to include Wollaston and most of Reindeer Lake.

Some additional information concerning the physiography of specific areas can be obtained from the five papers mentioned in the introduction.

MORPHOMETRY

The morphometric data for the twelve lakes under consideration are summarized in Table 1. The lakes are listed in a geographic sequence, first the four very large lakes which lie across the far north of the province and Frobisher which is also on the Precambrian Shield but close to its southern margin. Lac la Ronge, Hunter Bay and Amisk Lake all lie across the margin of the Shield. The last group of five lakes is south of the Shield and includes four Upper Churchill Lakes and Waskesiu, which is much farther south but still in the Churchill drainage. The measurements listed in Table 1 include most of those usually made by limnologists and one or two not often recorded.

The areas of these lakes vary widely, from Waskesiu 70 km^2 (27 mi^2) to Athabaska 7,900 km^2 (3,050 mi^2). Even Waskesiu is generally considered a large lake; thus, we are not dealing with any of the thousands of small bodies of water in this area. The depth range is moderate, from a mean depth of 5.1 m (15.5 ft) in Little Peter Pond to 26.0 m (79 ft) in Lake Athabaska. Maximum depths are also listed but they are less useful than mean depths; in fact, they may be definitely misleading. Thus the maximum observed in Reindeer Lake is 215 m (655 ft), but this depth occurs only in a small crater bay at the south end. Reindeer Lake is for practical purposes a much shallower lake than Athabaska, although the maximum depth in the latter is only 120 m (366 ft). It will be noted that, with three exceptions, the mean depths of these lakes are less than 18 m and are thus in what would be considered as the eutrophic range. However, most of them are oligotrophic for reasons other than morphology. Frobisher provides a striking example. Its mean depth of 5.5 m is similar to that of Little Peter Pond, but it is unlike the latter in almost every other characteristic.

Irregularity of the shoreline and the extent to which islands occur, are believed to have a profound effect on the ecological conditions in this series of lakes. The results of wide exposure to wind and the resulting vigorous water circulation are seen in the large lake, Athabaska, and in a lake of moderate size, Big Peter Pond. The effects of irregular shoreline and many islands in increasing the rich inshore environment are illustrated in Cree, Reindeer and Frobisher lakes. Lac la Ronge has the interesting combination of a northern part, broken and protected by many islands and a southern part with wide exposure to winds. To express these differences between lakes it is necessary to measure shore lengths for the lakes and the islands and to relate these to the areas of both. The shore development, that is, the relation of shore length to the circumference of a circle equal in area to that of the lake, is at least a partially satisfactory quantitative index to the condition which we are discussing. Shore development in our twelve lakes varies from 1.3 in Little Peter Pond, which has regular shoreline and is somewhat circular in outline, to 9.0 in Reindeer Lake which has a most intricate outline.

The number of islands in the lakes wholly or partly on the Precambrian Shield is impressive, ranging from 370 in Wollaston to more than 2,500 in Reindeer. In the lakes south of the Shield the number of islands is low, down to one in Waskesiu and none in Big Peter Pond. The area of islands is also worth recording since some of them are very large and some very small. (In our listing small, reef-like protrusions with little vegetative cover have not been recorded as islands.) The usual expression for island development or "insulosity" is the percentage of the area within the shoreline, occu-

pied by islands. This has been calculated and listed in Table 1. Since the existence of many islands has an effect similar to the possession of an irregular shoreline, it would seem that instead of the conventional expressions for shore development and insulosity one might use a calculation of shore development which includes the shoreline of the islands. With this calculation the value for Reindeer Lake rises from 9.0 to 16.5 and that for Cree from 6.5 to 13.6. On the other hand, for Athabaska, where the islands are numerous but relatively small, the change is only from 6.0 to 6.8. Thus of the several measurements dealing with shoreline and islands, the value for shore development including islands may be considered the most meaningful single item. Nevertheless, as Larkin (personal communication) has pointed out, this value may be misleading when used to compare lakes which differ greatly in area. In such cases a simple ratio of shore length to lake area is preferable.

Altitude and drainage areas are also listed in Table 1. The range of altitude is not great in this area, Waskesiu being the highest, 531 m (1,740 ft), and Athabaska the lowest, 213 m (699 ft). Waskesiu and Cree, lying at high altitudes, have relatively small drainage areas. Reindeer and Ile a la Crosse lakes, being far down in their drainage systems, have very large drainage areas. The area draining into Lake Athabaska at its east end is about 67,300 km^2 (26,000 mi^2). Additional large areas drain into it along its north and south shores. The Athabaska River drains a huge area in Alberta, but analyses of total solids show that most of this water passes across the west end of the lake and on down the Slave River with little mixing into the main lake. For this reason the drainage area for Lake Athabaska is not listed in Table 1.

The last item in Table 1 is the period of "flushing," or the time needed for an amount of water equal to the lake volume to pass through its outlet. This is a somewhat crude calculation based on the available data for average rate of outflow. It takes no account of rates of evaporation and the excess of inflow over outflow. From the limited data available, it seems unlikely that rate of flushing has much biological significance in very large lakes. However, in lakes such as Ile a la Crosse, where a theoretical exchange of water occurs in 9 months, there appears to be a lowering of the standing crops of organisms. This opinion is strengthened by recent studies on lakes lower down in the Churchill River, which have still shorter periods of flushing.

Seasonal and annual changes in water levels have been recorded for the lakes under consideration. The seasonal changes are usually between 0.3 and 1 m in extent and over a period of many years they may amount to 1.5 m. They are not believed to be of much importance in the productivity of this group of lakes and have not been recorded in Table 1. Of the twelve lakes, only Reindeer has its level considerably altered by artificial control, although Waskesiu has a small dam at the outlet to maintain a constant level.

PHYSICAL AND CHEMICAL INFORMATION

Information concerning the physical and chemical conditions in the twelve lakes appears in Table 2. The original observations were made over one or more summers and usually at weekly intervals and at two or more stations on each lake. From these extensive data, it has been necessary to select those which appear to be most helpful in characterizing the lakes. Thus, most of the values in Table 2 are seasonal averages, maxima and minima.

The first item is the mean temperature in the upper 10 m through July and August. This seems to be a very useful figure since it indicates the approximate temperature of the main productive zone through most of the summer season on these lakes. The range for this value, from 12.6°C in Wollaston to 17.7°C in Churchill Lake, is not wide, yet the sequence of mean temperatures will be found to follow very closely the order in which the lakes are placed according to their biological indices. The highest mean temperature for the whole lake (not just the 0–10 m stratum) is also shown. It is of interest in itself and is also used for calculating heat income. The maximum near-

TABLE 2. *Physical and chemical data for lakes in northern Saskatchewan*

	Athabaska	Cree	Wollaston	Reindeer	Frobisher	La Ronge	Hunter Bay	Amisk	Churchill	Big Peter Pond	Little Peter Pond	Ile a la Crosse	Waskesiu
Thermal features													
Mean temp. 0–10 m °C.*	13.4	14.9	12.6	14.2	17.0	16.6	16.0	15.8	17.7	16.3	17.4	17.5	17.4
Highest mean temp. °C.	10.0	14.1	11.1	13.0	18.0	17.0	14.0	15.5	19.2	18.5	21.0	15.9	18.3
Max. bottom temp. °C.*	4.8	10.1	5.8	6.5	18.0	12.5	9.2	12.0	18.0	15.0	18.5	17.4	14.9
Heat income, cal/cm^2 × 10^3	15.6	15.0	14.6	15.3	7.7	16.5	20.7	15.8	13.7	19.8	8.7	9.7	15.9
Stratification, degree	none	mod.	mod.	mod.	none	mod.	mod.	mod.	none	none	none	slight	strong
Stratification, duration	—	long	irreg.	long	—	long	long	long	—	—	—	brief	long
Dissolved Oxygen													
Average at lake bottom July–Aug. mg/L	9.7	9.3	9.7	8.3	7.0	5.7	8.9	4.3	6.0	3.3	6.4	4.9	2.9
Lowest % saturation	77	54	77	69	67	48	65	21	47	10	57	30	0
pH													
Average surface	7.2	7.0	7.2	7.2	8.1	8.2	7.9	7.7	8.1	8.2	8.2	8.1	8.2
Average bottom	7.2	6.5	6.8	6.8	7.6	7.7	7.5	7.0	7.5	7.2	7.8	7.5	7.4
Total solids ppm	58	27	35	39	79	149	118	88	136	138	144	185	188
Transparency													
Secchi disc av. m	5.6	7.8	6.8	7.0	1.7	4.5	6.2	3.8	2.1	2.5	1.9	2.7	3.1
Secchi disc range m	2.7–8.0	5.6–11.4	4.0–9.0	6.0–8.5	1.5–2.0	3.0–6.5	4.0–8.0	2.5–5.0	1.4–3.0	1.2–3.0	1.0–2.8	1.5–3.4	2.3–4.0
Color U.S.G.S. units	0	0	0	0	50	20	0	20	25	30	30	60	0

* for period July–August.

bottom temperature during July and August is low in the larger northern and high in the southern lakes of the group. There are, however, some irregularities such as Cree Lake with 10.1°C. This temperature was observed on August 24, 1955, at 46 m, at an exposed station. However, the temperature at 37 m at a protected station in Cree Lake remained as low as 5.2°C until September 3. Thus, the highest bottom temperature observed may depend on whether one uses the deepest station, whether this station is exposed or protected, and whether the thermal stratification happens to be destroyed before the arbitrary date set for the end of the "summer" season, in this case August 31.

The heat incomes listed in Table 2 are summer incomes, since the winter minimum temperatures are not known except in Lac la Ronge. However, the question is not whether summer heat incomes are as good as annual heat budgets but rather whether any such value is of much help in characterizing our lakes. In a recent paper (Rawson 1958) three lakes have been selected as having almost identical summer incomes (15,600 to 15,900 cal/cm^2). These are Lake Athabaska which is extremely oligotrophic, Amisk Lake which is intermediate and Waskesiu which is moderately eutrophic. In this instance the heat income, derived from highest mean temperature and mean depth, is certainly less instructive than the two separate values, and as we have indicated above, the mean temperature of the 0–10 m zone appears to be more useful than mean temperature of the whole lake.

The last of the features listed in Table 2 is an attempt to describe thermal stratification in qualitative terms as to degree and duration. Of the five lakes which are indicated as having no stratification, Frobisher is extremely shallow and its water is circulated throughout the summer at fairly high temperatures. Three other Upper Churchill lakes are deeper but widely exposed and they also show no stratification. Lake Athabaska is very deep and remains rather cold at the surface even at midsummer. Thus its temperature gradient is gradual, and at no time is there a region which approaches the condition described as a thermocline.

The vertical distribution of dissolved oxygen was followed throughout the summer season in each lake. However, for our purposes, the only feature of special significance is the amount of midsummer de-

pletion in the deep water. Thus, Table 2 includes the average amounts of oxygen near bottom during July and August and the lowest saturation value observed during this period. As would be expected, most of these northern lakes have well-oxygenated hypolimnia. Only in Wakesiu and Big Peter Pond is there any marked bottom stagnation and in the latter this condition is confined to a small area and short duration. Waskesiu, with the lowest amounts of oxygen in the series, is apparently too stagnant for lake trout, since they occur in Kingsmere, an adjacent and connected lake.

The hydrogen ion concentration of the various lakes has been indicated by the whole summer average for surface and bottom water. The lakes are mostly neutral to slightly alkaline, pH 7.0 to 8.2, with slight acidity developing in the deep water of some during the summer. The range of pH is not large and information concerning it is not of much use in classifying the lakes.

From the mineral analyses of the lake waters, we have included only the total dissolved solids determined by evaporation at 105°C. This simple determination seems to provide a useful index to the general edaphic conditions in our lakes. This is somewhat surprising since most limnologists would agree with Margalef (1958) that productivity is specially related to the minor constituents, nitrogen and phosphorus. He suggests that the major mineral constituents are useful in distinguishing limnological regions but of less use in typology based on productivity. Perhaps the apparent relation between total solids and productivity is largely artificial. However, evidence continues to accumulate to indicate that such a relation does exist, *e.g.* Rawson (1942, 1951), Möller (1949, 1955), Dunn (1954), Northcote and Larkin (1956) and Larkin and Northcote (1958).

Very low mineral content is found in the waters of Cree, Wollaston, Reindeer and Athabaska lakes, the most oligotrophic of our series. Considerably higher mineral content is found in the more productive lakes such as Waskesiu. It should be noted that the total solid content in these lakes varies somewhat, both seasonally and from year to year. Thus, the figures quoted are in most cases averages of several determinations. Although the total mineral content varies from 27 ppm in Cree to seven times this amount in Waskesiu, the proportions of the constituent ions are quite similar in the different lakes. Thus, a lake in this series with 100 ppm total solids would have the following approximate constitution: bicarbonate (HCO_3) – 85 ppm; calcium (Ca) – 17; magnesium (Mg) – 7; sulphate (SO_4) – 7; chloride (Cl) – 3; sodium (Na) – 2.5; silica (SiO_2) – 2.5; and iron (Fe) – 0.05 ppm. These lakes are thus of the carbonate type with plenty of calcium. Those on the Precambrian Shield have very soft water, with specific conductivities ranging from 29 to 89 micro-mho. Those south of the Shield are moderately hard and have specific conductivities from 200 to 280 micro-mho.

Transparency, or light penetration into the twelve lakes is indicated by the average of Secchi disc readings for the whole summer, usually late May or early September. It seems desirable also to record the range of the readings made in each lake. In the large lakes on the Precambrian Shield the average transparency runs from 5.6 m in Athabaska to 7.8 in Cree. In those lakes south of the margin the average is from 1.9 to 3.1 m. Frobisher, although on the Shield, is very shallow and has a moderately colored water. Its average transparency was the lowest in the whole series. In general, greater transparency is found in the more oligotrophic lakes, mainly because of the greater interference with light penetration by the plankton of the more productive lakes.

The water in most of these lakes would be described as colorless, but close examination reveals a few which have a slight yellowness. Water color, as measured by the United States Geological Survey scale, is recorded as the last item in Table 2. Color is most marked in the lakes of the Upper Churchill area, presumably because of the large amounts of muskeg (sphagnum bog) drainage in this low-lying area. The highest color values observed were 50 units in Frobisher and 60 in Ile a la Crosse lakes. These are still comparatively low and, with

TABLE 3. *Biological data for lakes in northern Saskatchewan*

	Athabaska	Cree	Wollaston	Reindeer	Frobisher	La Ronge	Hunter Bay	Amisk	Churchill	Big Peter Pond	Little Peter Pond	Ile a la Crosse	Waskesiu
Net Plankton													
Av. dry wt kg/ha	36.5	25.2	14.8	28.7	45	64.3	32.0	30.3	165	98	112	93	90.5
Water blooms	none	none	none	rare	rare	rare	none	rare	mod.	very heavy	heavy	slight	mod.
Bottom fauna													
Av. dry wt kg/ha	4.1	1.6	4.7	1.6	2.2	8.9	7.1	9.1	15.1	73.4	26.0	9.0	24.6
Av. nos. per m^2	1,275	274	814	1,442	722	742	2,192	2,844	1,076	5,640	2,807	1,807	837
Composition, %													
Chironomids	11	60	9	4	8	52	4	18	53	58	58	26	66
Amphipods	61	2	70	72	43	17	60	59	23	21	25	34	4
Sphaeriids	9	12	12	17	37	10	25	9	2	7	11	21	1
Oligochaetes	12	16	9	5	4	15	6	8	9	9	4	13	5
Mysis	few	v. rare	+	few	—	+	+	+	few	·	·	—	—
Pontoporeia	+	—	+	+	—	+	+	+	—	+	—	+	—
Fish/standard net													
Average number	103	96	64	68	38	163	95	66	101	250	122	129	119
Av. wt kg	44	47	45	46	27	71	57	26	47	127	70	67	61
(lb)	(97)	(103)	(99)	(102)	(59)	(156)	(126)	(57)	(104)	(281)	(153)	(148)	(134)
Composition, %													
Whitefish	56.2	30.5	42.1	54.4	0.3	40.3	60.6	11.0	3.0	25.3	0.8	3.3	15.4
Ciscoes	15.5	4.1	2.2	13.9	24.2	42.4	23.2	62.0	52.9	43.7	53.5	55.0	28.9
Trout	2.4	4.5	11.2	16.8	—	1.2	4.8	+	—	—	—	+	—
Pike	1.8	1.1	2.8	2.6	26.0	1.4	2.4	4.0	9.3	3.2	12.4	13.0	12.2
Pickerel	5.6	1.4	5.7	2.9	18.0	1.0	4.9	10.0	4.8	11.9	15.6	9.8	5.4
Longnose sucker	5.2	42.5	25.0	8.1	—	7.2	1.6	1.7	0.9	5.1	0.6	0.7	2.1
White sucker	2.0	11.5	6.0	0.5	31.2	3.2	1.0	8.0	23.8	8.0	14.8	13.2	14.1
Burbot	1.4	1.5	0.8	0.8	0.3	1.3	1.5	1.2	0.5	1.6	+	0.8	0.4
Commerc. fish prod.													
Av. kg/ha/yr.	0.43	1.03	1.18	1.2	2.2	1.1		3.3	3.4	5.6	6.7	3.4	7.8
(lb/ac/yr)	(0.38)	(0.92)	(1.05)	(1.1)	(2.0)	(1.0)	—	(2.9)	(3.0)	(5.0)	(6.0)	(3.0)	(7.0)
Years of fishing	20	11	12	12	15	29	—	20	10	15	15	15	10

the possible exception of Frobisher, we have no reason to believe that water color is an important factor in the productivity of this series of lakes.

BIOLOGICAL OBSERVATIONS

The average standing crop of net plankton is the first item listed in Table 3, which summarizes our observations on the biological conditions in the twelve lakes. The nets used were of #20 silk with about 68 meshes /cm (173/in). Their straining efficiencies were determined by comparison with 10-liter trap samples. Samples were taken at approximately weekly intervals throughout the summer months, at one or more representative stations in each lake. The average dry weight of plankton in the highly oligotrophic, northern lakes varies from 14.8 kg/ha in Wollaston to 36.5 in Athabaska. The richer lakes south of the Precambrian have from 90.5 kg/ha in Waskesiu to 165 in Churchill. More extensive data on the standing crops of plankton in lakes of western Canada were published in an earlier paper (Rawson 1953). In spite of the wide and sudden variations in the plankton crop and the difficulties of accurate measurement, it was demonstrated that characteristic oligotrophic lakes in western Canada had standing crops of plankton less than one-third the weight of those in typical eutrophic lakes.

Plankton samples from all twelve lakes have been examined microscopically and extensive counting done on some of the samples. In general, the plankton is dominated by diatoms and copepods. *Melosira* and *Asterionella* are the chief diatoms, followed by *Fragilaria* and *Tabellaria*. Green algae are present in small numbers and blue-greens, especially *Anabaena, Aphanizome-*

non and *Microcystis*, may be numerous. The copepods are represented by several species of *Cyclops* and *Diaptomus* and in most of the lakes by *Limnocalanus*. The commonest cladocerans are *Bosmina* and *Daphnia*. The rotifers *Keratella* and *Kellicottia* are dominant, followed by *Polyarthra* and *Conochilus*.

The dominant forms have been sent to appropriate authorities for species identification, and some attempt has been made to characterize and differentiate the plankton of these lakes. With minor exceptions this has been unsuccessful. Among the copepods *Cyclops scutifer* is common in the Precambrian lakes, Cree, Wollaston, Reindeer and Amisk, but does not occur in the five Upper Churchill lakes nor in Waskesiu. In these southern lakes, *Mesocyclops edax* is common. *Limnocalanus macrurus*, a supposedly relict species, is present in all of the lakes except Cree and Waskesiu. It would hardly be expected in eutrophic lakes such as Waskesiu but its absence from Cree is as surprising as, and possibly related to, the absence of another relict species, the amphipod *Pontoporeia affinis*, from the same lake.

Comments on the problem of algal indicators of trophic lake types were published in a recent paper (Rawson 1956). Differentiation of the lakes on a basis of the species composition of their plankton will require much more thorough investigation. There is, however, one feature of plankton composition, namely the presence of algal blooms, which is readily observed and which does have significance in our classification.

The presence and extent of algal blooms in the twelve lakes are listed in Table 3. Although blue-green algae, of the genera mentioned above, may be common in the big northern lakes, they are very rarely concentrated on the lake surface as blooms. By contrast, the Upper Churchill lakes and Waskesiu are characterized by heavy blooms. In Big Peter Pond Lake blooms of *Anabaena* and *Microcystis* extend over many square miles and often persist for many days in warm weather.

The quantities of bottom organisms in the various lakes are indicated both by dry weight and number per unit area. The average weights of bottom fauna are reasonably consistent with the amounts of plankton above and the fish catch indicated below. In the northern oligotrophic lakes the average weight of bottom organisms varies from 1.6 kg/ha in Reindeer Lake to 4.7 in Wollaston. Lakes of the margin of the Precambrian are intermediate with 7.1 to 9.1 kg/ha and those south of the margin, with the exception of Ile a la Crosse, have very much greater weights. The numerical values are much less consistent than the weights. Thus, Athabaska has an average of 1,275 organisms/m^2 and Waskesiu has only 836, yet the weight in Athabaska is just one sixth that in Waskesiu. Most of the organisms in Athabaska are small amphipods, *Pontoporeia*, while those in Waskesiu are very large chironomid larvae. Obviously the weight is a more useful value.

The numerical composition of the bottom organisms in the different lakes is also indicated in Table 3. In all the oligotrophic lakes, except Cree, amphipods are dominant, usually 60% to 70% of the total fauna. In all of the lakes south of the Precambrian, except Ile a la Crosse, chironomid larvae show a similar dominance. Lac la Ronge, being of moderate depth and not too cold, is like the southern lakes but its adjoining area, Hunter Bay, having great depth and colder water, has a 60% dominance of *Pontoporeia* like the northern oligotrophic lakes. Cree Lake, although deep and cold, lacks the only species of amphipod, *Pontoporeia*, which can inhabit this environment. Thus, it has an extremely poor bottom fauna, lowest in numbers of all the lakes and sharing with Reindeer Lake the lowest weight. This paucity of bottom organisms in Cree Lake is accentuated by the scarcity of *Mysis relicta*, another relict crustacean which is of considerable importance as fish food in most large northern lakes.

The fish sampling was carried on with standardized nets, 300 yards long and including 50 yards each of 1.5, 2, 3, 4, 5 and 5.5 inch stretched mesh. These were set for periods of approximately 24 hours in all areas and depths of the lake and through-

out the summer months. The average number of net sets per lake was about 45. It was not expected that this technique would ensure a reliable measure of the fish population. The vagaries of weather, fish movements and individual prejudice in the location of net sets combine to introduce a large element of chance. It is known that some lakes, in which we caught very few whitefish, produce commercial quantities of this species. Nevertheless, the values for average weights and numbers of fish in Table 3 show a fairly consistent relation to the other biological and physical measurements. As with the bottom organisms, the numbers of fish are less informative than their weights, although this discrepancy is much less in the fish. Further details of the gill net catches in these lakes are to be found in the papers on individual lakes and especially in the paper on the five lakes of the Upper Churchill (Rawson 1957). The average weight of catches in the four large oligotrophic lakes, recorded in Table 3, is from 44 to 47 kg (97 to 103 lb) per standard set. The catches in five lakes off the Precambrian range from 47 to 127 kg (104 to 281 lb) and average 74 kg (164 lb). The fish catches in the lakes on the Precambrian margin and Frobisher show wide variation.

A second kind of information about the fish catch is the numerical percentage of each species in the average catches. From the data in Table 3 it is apparent that the whitefish, *Coregonus clupeaformis,* is a dominant species in these lakes. The low percentages in the catch from four Upper Churchill lakes represent deficiencies in our sampling, since commercial records show the existence of large quantities of whitefish in these lakes. The ciscoes, *Leucichthys* spp, are also abundant, especially in the eutrophic lakes. In the northern lakes they make up a smaller percentage of the fish catch but are important as food for trout. The lake trout, *Cristivomer namaycush,* is the dominant piscivore in most of the northern lakes and is absent from most of those south of the Precambrian. It is of interest that it is also absent from Frobisher, a warm shallow lake on the Precambrian, and present in Kingsmere, a deep lake which drains directly into Waskesiu. The pike, *Esox lucius,* is a consistent inhabitant of all of these lakes but considerably more numerous in the south. In the northern lakes it is largely confined to shallow, inshore waters and warm bays. The walleye (locally known as pickerel), *Stizostedion vitreum,* has a similar extensive distribution and is even more confined in the north to warm bays and inflowing rivers. Two species of suckers are the main coarse fish in these lakes. In the north, the longnose sucker, *Catostomus catastomus,* which can occupy deep cold water, is the dominant form; while in the warmer southern lakes the white or common sucker, *Catostomus commersonii,* is abundant. The burbot, *Lota maculosa,* a minor piscivore, is present in small numbers throughout the series. The yellow perch, *Perca flavescens,* is present in all the lakes but more numerous in the south. The grayling, *Thymallus signifer,* is found only in the four large northern lakes, Athabaska, Cree, Wollaston and Reindeer.

Rates of growth were determined in each lake for the four important species, whitefish, trout, pike and pickerel. These were compared to see whether the growth rates of a species in different lakes showed any relation to amounts of plankton, bottom organisms or fish. Although some species grew at quite different rates in the various lakes and, in a few instances, species grew slower in the cold northern lakes, no clear-cut order was observed. Thus, the growth rates of fish do not appear to be useful indicators of productivity in these lakes.

The average rate of commercial fish production is the last item in Table 3. This, of course, reflects the intensity of fishing as well as the productive capacity of the lake but it is an important item in fisheries management and, from the biological viewpoint, it is at least a measure of actual production whereas our other biological measurements are limited to the standing crop. In general, commercial production averaged about 1.1 kg/ha in the northern oligotrophic lakes and from 3.4 to 7.8 kg/ha in the richer southern lakes. This difference, of about 1 to 5, is a wider spread than that between our test-net catches on these groups of lakes.

TABLE 4. *Biological and physical ranking of northern Saskatchewan lakes*

	Mean depth	Mean summer temperature 0–10 m	Transparency (Secchi disc)	Average bottom oxygen (July–Aug.)	Total diss. solids	Physical "score" of possible 65	Quantity of plankton	Quantity of bottom fauna	Weight of fish per standard net	Biological "score" of possible 39
On Precambrian										
Wollaston	3	1	3	1	2	*10*	1	5	4	*10*
Cree	5	4	1	3	1	*14*	2	1	6	*9*
Reindeer	4	3	2	5	3	*17*	3	2	5	*10*
Athabaska	1	2	5	2	4	*14*	6	4	3	*13*
Frobisher	12	9	13	6	5	*45*	7	3	2	*12*
Across Margin										
Amisk	7	5	7	11	6	*36*	4	9	1	*14*
Hunter Bay	2	6	4	4	7	*23*	5	6	8	*17*
La Ronge	8	8	6	9	11	*42*	8	7	12	*27*
On Glacial Drift, South of Precambrian										
Churchill	10	13	11	8	8	*50*	13	10	7	*30*
Ile a la Crosse	11	12	9	10	12	*54*	10	8	10	*28*
Little Peter Pond	13	11	12	7	10	*53*	12	12	11	*35*
Big Peter Pond	6	7	10	12	9	*44*	11	13	13	*37*
Waskesiu	9	10	8	13	13	*53*	9	11	9	*30*

The more remote location of the four large northern lakes and consequent higher costs of transportation, has reduced the fishing pressure and has led to a fishery which selects trout and avoids whitefish. Undoubtedly, the northern lakes would be capable of much increased production if all desirable fish species were used. It seems probable, however, that under equally favorable conditions for production, rich southern lakes like Big Peter Pond would continue to produce several times as much fish per unit area as the four big northern lakes.

AGREEMENT OF PHYSICAL WITH BIOLOGICAL CHARACTERISTICS

From the above considerations of physical, chemical and biological data, it is possible to select the more valid and essential measurements with which to characterize our lakes. The physical and chemical values selected include mean depth, mean temperature of the upper ten meters, mean transparency, average bottom oxygen in July and August, and total dissolved solids. Our best biological measurements seem to be the average standing crops of plankton and bottom organisms and the average weight of fish taken in standard gill nets. Casual observation indicates that the deep, cold, clear lakes with low mineral content have lower crops of plankton, bottom organisms and fish, while shallow, warm and turbid lakes with high mineral content have heavy biological crops. The extent of this correspondence can be tested readily by ranking the bodies of water from 1 to 13 for each of these characters. This has been done in Table 4. Also five physical and chemical rankings have been added to obtain a physical "score" and three biological grades to get a biological "score" for each lake. With a single exception (Frobisher) the physical scores of the thirteen bodies of water fall into three distinct groups. Scores for the large lakes on the Precambrian are the lowest ranging from 10 to 17. The marginal lakes run from 23 to 42 and those of the glacial drift from 44 to 54. Frobisher Lake is a striking exception. It lies on the Precambrian, but, unlike the others, it is

shallow, warm and turbid, thus accumulating a score of 45. The biological scores fall, without exception, into three corresponding groups, the Precambrian group with 9 to 13 points, marginal lakes with 14 to 27, and southern lakes with 28 to 36.

There are, of course, many other ways in which these data could be analysed. Since the measurements are mostly averages and approximations rather than exact determinations, the calculation of mathematical correlations is not justified. There might, however, be some merit in determining the average amounts of plankton, bottom organisms and fish, in the five lakes on the Precambrian Shield and comparing these with the averages for the five lakes on the glacial drift. These data, extracted from Table 3, are as follows:

	Av. for 5 Precambrian lakes	Av. for 5 lakes on glacial drift	Ratios
Plankton, av. dry wt in kg/ha	30	111	1:3.7
Bottom fauna, av. dry wt in kg/ha	2.8	29.6	1:10.6
Fish, av. wt net in kg	42	74	1:1.8

It is evident from these values that the standing crops of living organisms are several times greater in the drift lakes than in those of the Precambrian. Further speculation on the meaning of these ratios should be tempered by the realization that net plankton is only part of the total plankton, that the gill-net catches only the larger fish, and that we are dealing with standing crops rather than with rates of production.

The method of ranking lakes according to amounts of plankton, bottom organisms and fish, and summing the ranks to get a biological score is somewhat related to the procedures of several other workers. Northcote and Larkin (1956) developed a means of obtaining bio-indices for one hundred lakes in British Columbia (see also Larkin and Northcote 1958). In those studies the clearest positive correlation was found between dissolved solids and crops of plankton, bottom fauna and fish. The relation between mean depth and quantities of plankton and bottom fauna was less marked and no climatic correlations were observed. The one hundred British Columbia lakes represent ten limnological regions and a wide range of climate and altitude. Our twelve lakes in Saskatchewan do not vary greatly as to climate or altitude and they are located in a region where essentially only two sets of environmental conditions are represented. In contrast, the British Columbia lakes showed a variety of individual differences in such things as quality of dissolved nutrients, exposure to wind action and fluctuation in water level; in short all of those features which reflect the diversified geography of a mountainous region. Thus, it is not surprising that, in these Saskatchewan lakes, we find what appears to be a more consistent agreement between biological and physical indices.

Reimers *et al.* (1955) used a method of ranking in an analysis of results from ten small alpine lakes in California. In this study, grades of physical, chemical and invertebrate abundance were in almost complete disagreement but the growth rate of trout (three species) showed a high positive correlation with total dissolved solids.

The extent of the agreement between the biological and physical ratings provides some measure of assurance that the selected measurements are capable of indicating trophic differences in our lakes. It is hoped that this information, together with the results of commercial fishing referred to above, will be effective in estimating the capacity of the lakes to produce fish.

CRITICAL FEATURES IN INDIVIDUAL LAKES

In comparing and ranking these lakes as to physical and biological characteristics, special features emerged which seemed to be unusually important in the productivity of particular lakes. The following instances of such key factors may be cited.

Big Peter Pond Lake has a mean depth of 13.7 m, a very heavy bottom fauna (mainly *Tendipes plumosus*) and marked water blooms. These are all clear evidence of eutrophic condition but, unlike typical eutrophic lakes, Big Peter Pond is not

thermally stratified and has no bottom stagnation. Its area is more than 520 km² and its shore development only 1.5. Thus, it is completely windswept and continuously circulated. Stangenberg (1953) describes a similar situation in Narocz Lake, Poland, and suggests that it should be termed pseudo-oligotrophic, a term which we regard as unnecessary. It appears that a nominally eutrophic lake continuously mixed by winds becomes exceptionally productive, in a manner somewhat analogous to a culture flask subjected to continuous shaking. It is thus not surprising that Big Peter Pond Lake has produced fish at a very high rate for the past forty years. Waskesiu Lake with an identical physical score and similar edaphic conditions but strong thermal stratification is distinctly less productive than Peter Pond.

Ile a la Crosse Lake has the highest physical score of any in Table 4, yet it has the lowest quantity of bottom fauna and the lowest biological score in that group of five lakes south of the Precambrian. The probable explanation of this lowered production is a physical factor not included in Table 4. The "flushing time" for Ile a la Crosse Lake is shown in Table 1 as 9 months, the shortest in the whole series. It is suggested that the tremendous water flow, coming into the lake from the Upper Churchill and from a vast river system to the south, flushes out the new-formed plankton products before they can be fully utilized. Observations, not yet published, on "river" lakes lower down in the Churchill system tend to support this explanation. The importance of flushing as a factor reducing the productivity of lakes has been demonstrated by McMynn and Larkin (1953), Robertson (1954), and Gorham (1958).

Cree Lake has been described above as lacking *Pontoporeia,* the only amphipod in this region capable of inhabiting deep cold water. In other northern lakes this species provides more than half the food of the commercially important whitefish. The fish catch in test nets in Cree was as heavy as in any other of the Precambrian lakes, but 54% of this catch was made up of unmarketable suckers. Thus, the absence of this key food organism appears to be a serious handicap in the commercial fish production of Cree Lake.

Frobisher Lake appeared in Table 4 as very unlike the other four Precambrian lakes in its physical score. Shallowness, turbidity and high temperature are the main contributors to this high score. Referring back to Table 1, it will be seen that Frobisher has the highest insulosity (27.5%) of all the lakes. It is composed of 313 km² of water broken into narrow channels and bays by 190 km² of islands. While conditions in Frobisher Lake stand in marked contrast to the four deep northern lakes, there are undoubtedly many others like it on the Precambrian Shield.

LAKE TYPES AND REGIONAL LIMNOLOGY

That the five lakes on the Precambrian Shield are definitely oligotrophic is evident from both physical and biological data summarized above in Table 4. The five lying south of the Shield are clearly eutrophic, although not all equally productive. The three on the margin of the Shield are intermediate but show some interesting differences among themselves. Amisk Lake and Hunter Bay have intermediate physical scores but their biological ratings overlap with those of lakes on the Precambrian and their biological scores are only slightly higher than those of the Precambrian group. Lac la Ronge, however, approaches the southern group both in biological and physical characteristics. It could safely be termed mesotrophic.

The oligotrophy of the Precambrian group of lakes would seem to be the combined result of several circumstances. With the exception of Frobisher, they are large and fairly deep and thus oligotrophic for morphometric reasons. They tend also to have less mineral inflow from their rocky or sandy drainage areas. This unfavorable edaphic condition is reflected in their total dissolved solids which average less than half those of the southern group. In the Precambrian region also air temperatures are low and summers short. Thus in this group morphometry, edaphic situation and climate are harmonic for oligotrophy.

Frobisher Lake is the unusual member of the Precambrian group. It is shallow, warm and fairly turbid, yet its biological indices show oligotrophy, for its biological score is no higher than that of Lake Athabaska. Since it is shallow and subject to essentially the same climate as eutrophic lakes like Big Peter Pond, it is reasonable to attribute part of its low productivity to unfavorable edaphic situation; its total solids are only 79 as compared to 136 in Churchill Lake. Since it is also somewhat colored and has low light penetration, it is probable that it also suffers from some degree of dystrophy.

In considering the factors affecting the three marginal lakes mentioned above, it should be noted that Amisk and Hunter Bay receive almost all their drainage from the Precambrian and thus have relatively low total solids. La Ronge, on the other hand, receives most of its inflow from the drift area to the south and has higher total solids. This corresponds with the biological scores of 14 and 17 in Amisk and Hunter as compared to 27 in La Ronge. The biological differences between Hunter Bay and La Ronge are, no doubt, partly due to this edaphic factor but they are accentuated by the considerable difference in their mean depths, 20.7 m in Hunter Bay and 12.7 m in Lac la Ronge.

The eutrophic condition in the five lakes south of the Shield appears to be mainly the result of favorable edaphic and morphometric conditions. Other studies such as those of Rawson and Moore (1944) and Mendis (1956) have shown that lakes with high total solids in the parkland and grassland areas have relatively heavy biological crops. But not all lakes in the area are eutrophic. Kingsmere, which lies just north of Waskesiu and drains into it, is distinctly oligotrophic (Rawson 1936). Its mean depth is 21 m, as compared to 11.1 in Waskesiu, and this is sufficient to render it oligotrophic in spite of high total solids and a climate identical with that of Waskesiu. Thus, shallow depth may intensify, or greater depth overpower, the natural tendency to eutrophy which depends primarily on the mineral content.

It should be noted that the edaphic influence can be indicated by using specific conductivity instead of total solids. The investigations of Dunn (1954) referred to above, made use of conductivity to differentiate between twelve oligotrophic and eutrophic lakes in Denmark. She found that clearly eutrophic lakes had conductivities greater than 200 micro-mho and those which were oligotrophic less. The eutrophic lakes in the present series have conductivities from about 200 in the Upper Churchill group to 280 micro-mho in Waskesiu. The oligotrophic lakes on the Precambrian range from 29 in Cree to 107 in Frobisher. Amisk, lying across the boundary, has 125 micro-mho.

It is indicated that air temperatures are somewhat lower and growing seasons shorter for the four large lakes in the northern part of the province and that this may contribute to their lower production as compared to lakes in the south. The latter group of eight lakes all lie in the Churchill Valley, where climate is relatively uniform. Thus, climate would not be expected to affect the differences between Frobisher, the marginal lakes and those south of the Shield. However, in individual lakes, climatic influence may have great importance, as, for instance, in Big Peter Pond where continuous summer mixing is believed to increase capacity for fish production.

Studies of the present series of twelve large lakes in Northern Saskatchewan combine with earlier studies of lakes in the middle area of the province to provide an introduction to the regional limnology of the area. To complete the general picture, it will be necessary to investigate also a series of small and medium-sized lakes from the thousands which occur on the Precambrian Shield.

SUMMARY

1. Twelve large lakes in Northern Saskatchewan show a wide range in their standing crops of living organisms. Five eutrophic lakes on the glacial drift have standing crops of plankton, bottom organisms and fish, several times as great as those of five oligotrophic lakes on the Precambrian Shield. Lakes lying across the margin of

the Shield are intermediate, or mesotrophic.

2. It is suggested that the underlying reason for low crops on the Shield lakes and higher crops on those to the south is edaphic, *i.e.* dependent on the availability of chemical nutrients derived from the watersheds. Since most of the northern lakes are deep and most of those south of the Shield are shallow, this morphometric difference accentuates the primary or edaphic influence. The four farthest north lakes are subject to a slightly colder climate and shorter growing season, thus climate also may contribute a little to the difference in biological production.

3. Comparisons between individual lakes of the Precambrian group, and especially the unique features of Frobisher Lake, tend to suggest that in this group, morphometric conditions may be somewhat less effective than edaphic. Comparison of conditions in the five lakes on the glacial drift suggest that in one instance, Big Peter Pond, continuous mixing of an essentially eutrophic lake greatly increases its productivity while in another, Ile a la Crosse, rapid flushing results in a marked lowering of production.

4. From a wide range of observational data it has been possible to select eight values (three biological and five physical) which appear to be most useful in classifying these twelve lakes. The device of ranking each lake with respect to these values and comparing their sums as physical and biological scores also gives promise of utility, especially where a primary purpose of the limnological investigation is to understand and manage the fish production in a group of lakes.

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A METHOD FOR DEVELOPING BRACHYURAN EGGS *IN VITRO*[1]

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ABSTRACT

The larvae of six species of Brachyura have been successfully hatched by detaching the eggs from the female, placing them in compartmented boxes, and maintaining them on an Eberbach variable speed shaker at constant temperatures at different salinities. In addition to providing thousands of normal larvae of known species for experimental purposes, the method has the following advantages: it provides adequate aeration, prevents the spread of fungi and protozoans throughout the egg mass, and permits the use of a relatively small number of eggs from the same animal in a limited space.

INTRODUCTION

Most studies on the larval development of the Brachyura have been based on reconstructions from planktonic material or on zoeae hatched from the female in the laboratory (Hyman 1920, 1924; Connolly 1925; Lebour 1928; Chamberlain 1957). In many cases only the first zoeal stage has been described because of the inability to maintain the larvae in the laboratory (Aikawa 1929). Detached eggs of only a few species of Brachyura have been hatched (Cannon 1923, *Cardisoma armatum;* Lochhead and Newcombe 1942, *Callinectes sapidus*) but none have survived beyond the first molt. Studies on the effects of salinity and temperature on larval development, acclimation to changes in environmental factors, and studies to determine the stages in the larval development of the Brachyura often require a satisfactory method of hatching zoeae from the eggs of a limited number of ovigerous females over a wide range of environmental factors.

The objectives of the present study have been to investigate the use of a variable speed shaker (Costlow *et al.* 1959) as a means of aerating detached eggs to assure proper development and hatching of zoeae from the eggs of a variety of Brachyura, and to determine if the eggs can be maintained at different salinity-temperature combinations on the shaker.

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METHODS

The egg mass, or "sponge," was removed from females of six species of Brachyura: *Callinectes sapidus* Rathbun; *Hepatus epheliticus* (Linnaeus); *Menippe mercenaria* (Say); *Pilumnus sayi* Rathbun; *Portunus gibbesii* (Stimpson); and *Portunus sayi* (Gibbes). The pleopods bearing the eggs were placed in small bowls of sea water, 30‰, and the strands of eggs were then cut from the pleopods with fine scissors, then further dissociated with glass needles into groups of about 100–1000 and transferred to freshly filtered water of the same salinity. After the eggs were washed in a third bowl, they were placed in compartments of plastic boxes containing approximately 20 ml of sea water (30‰) with 200,000 units of penicillin per liter. The surface area of each compartment was approximately 9 cm^2. If a variety of salinities were desired, the eggs were gradually changed into lower or higher salinities before placing them in the final salinity of the compartmented boxes. The boxes were placed on an Eberbach variable speed shaker (110–120/min) and maintained at either 22° or 25°C in a culture cabinet. The eggs were examined daily but the water was not changed. The detached eggs of all 6 species were maintained on the shaker for periods of not less than 3 days (*Portunus sayi*) nor more than 11 days (*Callinectes sapidus*) prior to hatching of the zoeae.

One intact anterior pleopod of *Callinectes sapidus,* bearing at least 100,000 eggs, was maintained in approximately 100 ml of sea

water in a circular, covered bowl on the shaker. Prior to hatching this water was changed every third day.

When hatching occurred some zoeae were transferred to separate plastic compartmented boxes containing water of the same salinity plus recently hatched *Artemia* nauplii and fertilized *Arbacia* eggs and the boxes were returned to the shaker. Fresh food was added daily and the zoeae were changed to freshly filtered sea water on alternate days. Other zoeae were maintained in small finger bowls on the same water and food but they were not shaken.

RESULTS

Hatching of the zoeae of the 6 species of Brachyura was observed at various periods of the day and night. Even at any one salinity there was some variation in the time of hatching. The per cent hatching was not determined for each compartment but vigorous zoeae were found swimming in compartments containing from 100 to 1000 eggs. One hundred per cent hatching of viable eggs, determined by counting the empty egg cases in the compartments, was observed in groups of from 100 to 1000 eggs. In the covered bowl, containing the intact pleopod and attached egg mass, thousands of zoeae hatched. Occasionally the eggs within one or two compartments of each box would deteriorate prior to hatching. In these compartments the water was found to contain in some cases a bloom of ciliates and in other cases fungi associated with the eggs. Although some larvae of *Callinectes sapidus* hatched as "pre-zoeae," most of the zoeae of all species emerged from the egg as first stage zoeae. Successful hatching of the zoeae from the eggs of all 6 species of Brachyura occurred on the shaker, and the zoeae continued to pass through successive stages of larval development.

DISCUSSION

In most previous studies on brachyuran larvae hatched in the laboratory the ovigerous females have been segregated and the larvae removed at the time of hatching. With some species this method may prove satisfactory but numerous difficulties can arise. Coffin (1958), rearing the larvae of *Pagurus samuelis* (Stimpson), noted that unless the water were changed frequently immediately prior to hatching the zoeae would emerge in a weakened condition or die soon after liberation. Knudsen (1958) confirmed this observation in his studies on the larval development of *Lophopanopeus leucomanus leucomanus.* In standing water, even though aerated, the possibility of increasing the growth of deleterious fungi, such as *Lagenidium callinectes* Couch, is enhanced. Previous workers (Sandoz, Rogers, and Newcombe, 1944) have noted that fungus infected eggs either failed to hatch or produced "pre-zoeae" which died after 48 hours. Rogers-Talbert (1948) noted that older egg masses are more heavily infected and that transmission of the fungus in the laboratory is extremely rapid on either intact ovigerous females or in isolated groups of eggs.

In addition to the danger of infection by fungi and the effects of stagnant water on the zoeae, some crabs, such as *Callinectes sapidus,* will frequently destroy their entire egg mass by tearing it with their pereiopods, either prior to hatching or shortly after some of the zoeae have been liberated (personal observations).

Some attempts have been made to hatch brachyuran larvae from eggs which were detached from the female. Cannon (1923) reported the successful hatching of detached *Cardisoma armatum* eggs in brackish water and in artificial sea water but none of the zoeae lived to molt. Truitt (1939) was unable to hatch *C. sapidus* eggs when they were detached from the female but subsequent workers (Lochhead and Newcombe 1942; Sandoz and Rogers 1944; and Rogers-Talbert 1948) reported hatching of from 5 to 90% with eggs of this species. Lochhead and Newcombe (1942) utilizing a variety of containers, obtained the highest per cent hatch from the largest number of eggs when shallow pans were used. They found that approximately 8 eggs per square centimeter of surface produced the best results. Sandoz and Rogers (1944) reported "satisfactory results" with approxi-

mately 50 eggs per square centimeter. In the present study the maximum number of eggs per compartment was 1000, approximately 110 per square centimeter, and thousands of zoeae were obtained from the eggs of those 6 species used. By segregating eggs in individual compartments the spread of fungi or ciliates was reduced and confined within the compartment.

The method allows one to subject the eggs of one female to a wide variety of controlled environmental conditions. Thus, if one obtains an ovigerous female of a relatively uncommon species the total loss of all zoeae due to an unfavorable salinity-temperature combination is avoided. If the eggs are obtained at an early stage of development and if hatching occurs in a variety of salinity-temperature combinations, the eggs and zoeae are known to have been acclimated to the experimental conditions. For example, it has been reported that eggs of *Callinectes sapidus* hatched at 32‰ would not complete zoeal development and metamorphose to the megalops (Costlow and Bookhout 1959). In the present study it was found that if the eggs are maintained at 34‰ throughout a major portion of the estimated two week embryonic period, metamorphosis to the megalops at 34‰ can be achieved. A third advantage of this method for laboratory purposes is that it allows one to obtain zoeae approximately one month before they are available in nature. Ovigerous females of *C. sapidus*, bearing recently laid egg masses, are first found in early April in the Beaufort, N. C. area. Females with dark sponges, indicating that development has progressed and that hatching is imminent are not found for at least another 4–6 weeks in the natural environment. If the eggs are removed from the females which are available in early April, segregated in compartmented boxes, and the temperature of the water gradually increased above that of the outside waters, hatching of the segregated eggs will occur approximately one month in advance of an intact egg mass which is maintained at normal water temperature for this period of the year.

SUMMARY AND CONCLUSIONS

The larvae of 6 species of Brachyura, *Callinectes sapidus* Rathbun, *Hepatus epheliticus* (Linnaeus), *Menippe mercenaria* (Say), *Pilumnus sayi* Rathbun, *Portunus gibbesii* (Stimpson), and *Portunus sayi* (Gibbes), have been successfully hatched by detaching the eggs from the female, placing them in compartmented boxes, and maintaining them on an Eberbach variable speed shaker at constant temperatures at different salinities. In addition to providing thousands of normal larvae of known species for experimental purposes, the method has the following advantages: it provides adequate aeration, prevents the spread of fungi and protozoans throughout the egg mass, and permits the use of a relatively small number of eggs from the same animal in a limited space.

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THE CAUSE OF A METALIMNETIC MINIMUM OF DISSOLVED OXYGEN[1]

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ABSTRACT

Coincident with a condition of rapidly increasing eutrophication, Lake Washington, a large, deep lake, near Seattle, is exhibiting an increase in the magnitude of a metalimnetic depletion of dissolved oxygen. Possible causes of this depletion are examined, and the conclusion is that the respiration of a metalimnetic population of non-migrating copepods is the prime agent. Calculations are presented in support of this conclusion, and chemical properties of the notch are compared with those of a hypolimnetic notch due to morphometric causes, to provide further evidence. The recent increase in magnitude of the phenomenon is considered to be due to the increase in numbers of copepods.

On August 9, 1913, Kemmerer, Bovard, and Boorman (1923) made the first recorded determinations of dissolved oxygen in Lake Washington. At that time nearby Seattle was small (population about 250,000), and this large lake (8760 ha; mean depth 33 m; maximum depth 66 m) was oligotrophic. Today, Seattle is considerably larger (population about 750,000), and Lake Washington is eutrophic. One of the most interesting changes associated with this sewage-generated eutrophication of the lake (Edmondson *et al.* 1956) has been the continued increase in size of a metalimnetic minimum of dissolved oxygen. Most of the data to be presented concerning the minimum have been gathered as part of a study of this domestic eutrophication.

Figure 1 illustrates the change over the last 25 years. The minimum usually appears at the beginning of June and grows progressively stronger until it disappears toward the end of October. The lowest dissolved oxygen concentration ever observed in the notch was 2.2 mg/L at 15 m on October 1, 1957. Although depletion proceeded at a faster rate in 1958 than in 1957, the lowest figure observed in 1958 was 2.9 mg/L at 11 m on August 18. This failure to fall below the 1957 value probably results from the windier conditions in 1958. The relatively rapid rate of increase of magnitude of the notch in recent years reflects the general pattern of the eutrophication of the lake.

This phenomenon of progressive increase of an oxygen notch has been exhibited by other fertilized lakes (Ohle 1951; Thomas 1958), but no satisfactory explanation has been put forward. The data on Lake Washington support an early hypothesis of Minder (1923), and may help in understanding these other situations.

CAUSES OF OXYGEN MINIMA

There are three possible causes of midwater oxygen minima: 1) interposition of water masses having low dissolved oxygen content between masses containing more dissolved oxygen; 2) morphological features of the basin associated with horizontal water movement; and 3) oxygen-consuming events occurring *in situ*.

The first of these is relatively rare in lakes, although it probably occurs in the sea. Ellis (1940) concluded that such a situation occurred in Elephant Butte Reservoir, New Mexico, as a result of the interaction of three major factors: 1) flows produced by the draw-off at the foot of the dam; 2) disturbances caused by the shape of the impoundment, and deflections by a submerged obstruction; and 3) variability in the composition and volume of the waters entering the lower lake from the upper lake.

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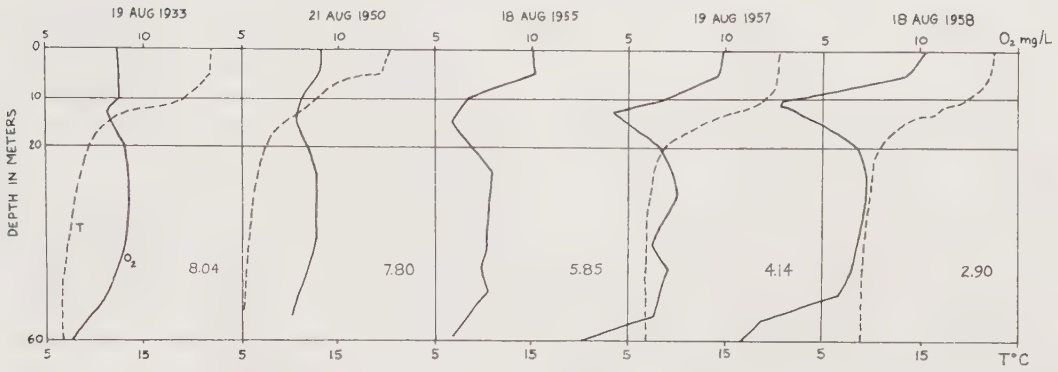

FIG. 1. Dissolved oxygen and temperature in Lake Washington on approximately the same date in 5 different summers. In each case the figure represents the lowest concentration of dissolved oxygen (in mg/L) found in the metalimnion on that date.

Wiebe (1939) recorded a somewhat similar situation in Norris Reservoir, Tennessee.

The second cause relates to Alsterberg's (1927) contention of horizontal movements in the hypolimnion. It depends upon the fact that where the hypsographic curve of a basin flattens there will be a stratum in which the area of mud per unit volume of water is much increased, resulting in a disproportionate uptake of oxygen by the mud in contact with that stratum. This type of oxygen minimum is fairly common. Hutchinson (1938) studied such a phenomenon in Linsley Pond, with respect to the distribution of bicarbonate. Åberg and Rodhe (1942) found a situation in Skärshultsjön, Sweden, where the oxygen minimum was accompanied by a maximum of carbon dioxide, bicarbonate, color, oxidizable matter, and decrease in pH. Other examples are in the Zürichuntersee, as noted by Thomas (1958), and in the oligotrophic Feforvatn in the mountains of Norway. The latter exhibits this phenomenon at two depths, although Strøm (1931) makes no mention of it in his paper on the lake.

The third cause received its classical exposition from Birge and Juday (1911). They believed that metalimnetic oxygen minima result from the slowing of falling materials by the colder water. This hypothesis was endorsed by Thienemann (1928), but Hutchinson (1957) reasons that only when a particle descends below the epilimnion into the less turbulent layers is its descent assured. However, in spite of this sound theoretical objection there is some evidence for the occurrence of the phenomenon. Whitney (1938) found that with few exceptions the lakes which he studied showed a sudden drop to a minimum transparency just below the epilimnion. His measurements unfortunately were not accompanied by oxygen determinations. Very recently Wood (1959) visually observed a very thin layer of particulate material accumulating in the thermocline region of a small lake. Here too there were no oxygen measurements. Miyake and Saruhashi (1956) have noted that the oxygen minimum in the sea appears most frequently in the water layer with a density of $\sigma_t = 27.2$ to 27.3.

A somewhat different approach to the problem of oxygen utilization *in situ* was suggested by Minder (1923). He advanced the idea that some minima can be traced to high zooplankton concentrations. However, his supporting evidence was weak and the idea was criticized strongly by Thienemann (1928). Whitney on one occasion did find a maximum of *Daphnia* coinciding with the layer of minimum transparency, but since he did not measure oxygen this provides no real support for Minder's view. On the other hand, Riley (1951) has offered evidence that the mid depth oxygen minima in the sea may indeed be caused by unusually large concentrations of zooplankton.

While not strictly in the category of zoo-

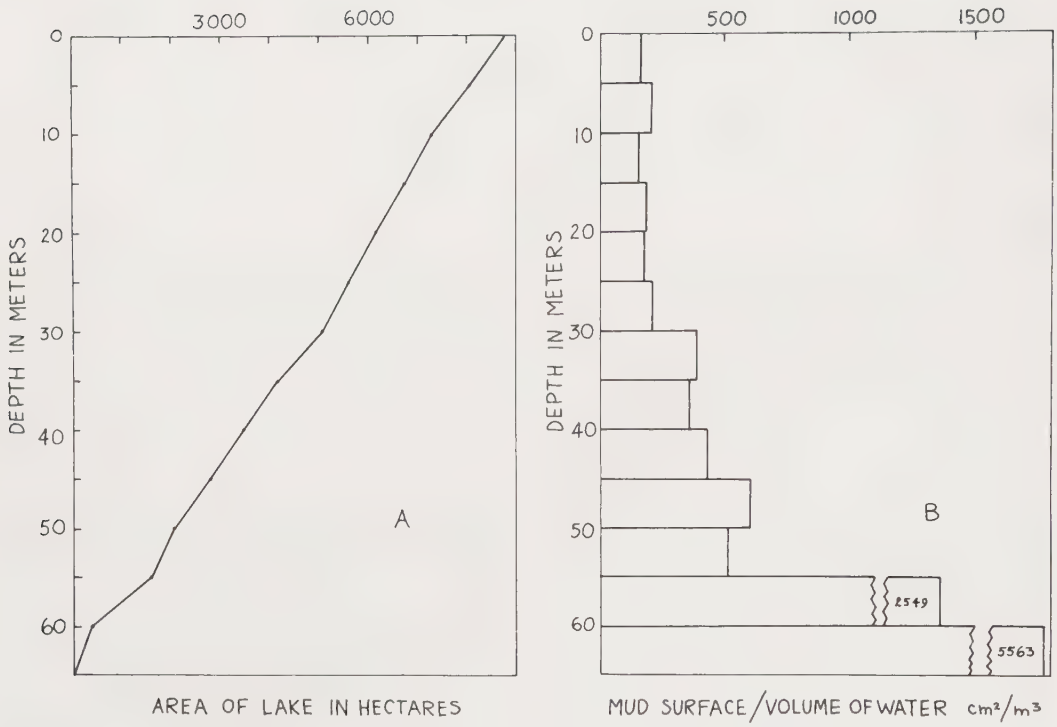

FIG. 2. A. Graph showing the area of Lake Washington at different depths. B. Plot of mud surface per volume of water for different strata in Lake Washington. For each stratum the total area was taken as the difference in area between the top and bottom of the stratum.

plankton, bacteria must also be considered. Kusnetzow and Karsinkin (1931) concluded that the metalimnetic oxygen minimum in Lake Glubokoje was caused by a metalimnetic maximum of these organisms. Although the distributions did not coincide perfectly, their results are impressive when the difficulties involved in direct counts of bacteria in lake water are taken into account.

Finally, Ohle (1958) has recently suggested that minima may be caused by the biogenic oxidation of rising methane bubbles and dissolved methane.

CAUSES OF THE MINIMUM IN LAKE WASHINGTON

With these facts and hypotheses in mind the data for Lake Washington were examined to determine the cause of its metalimnetic oxygen minimum.

The very nature of the metalimnetic minimum precluded its being due to the first cause of interposition of water masses. The depletion takes place over the entire lake at the same depth, and is progressive throughout the summer. This would suggest a long term cause as opposed to an episodic one. The many hundreds of dissolved oxygen determinations give no suggestion of large scale movements which could result in such a minimum.

To evaluate the significance of the second possible cause, the hypsographic curve was drawn for Lake Washington (Fig. 2a). Three shelf areas do exist in the lake; at 5 to 10 m; 30 to 35 m; and 55 to 60 m. The picture is clearer in Figure 2b where the data are plotted as mud surface per volume of water. Due to the volumes involved, the shelf at 55 to 60 m is replaced by a maximum of oxygen-absorbing surface at 45 to 50 m. There is also a suggestion of a slight maximum at 15 to 20 m.

It is tempting to suggest that the shelf at 5 to 10 m is responsible for the oxygen mini-

mum, but this is unlikely for several reasons. During most of the summer the epilimnion includes the upper 10 m, and any shelf effect, even if due to a larger shelf than found here, would be obscured by mixing. Also, even while the oxygen concentration is decreasing, the notch tends to move downward during the summer from its earliest depth at about 10 m to as deep as 25 m in the fall. Finally, the observations of chemical substances other than dissolved oxygen are not in harmony with the shelf hypothesis. However, this will be discussed later.

Of the other shelves, the maximum at 45 to 50 m is probably too near the bottom to make its effects distinguishable, but the one at 30 to 35 m has an effect (see August 19, 1957, Fig. 1) and provides an excellent opportunity for contrast with the metalimnetic phenomenon. Although evident from as early as mid June to as late as the end of October, the hypolimnetic notch never achieved a magnitude approaching that of the metalimnetic minimum. The greatest depletion over the expected concentration (obtained by interpolation between points above and below) was about 1 to 1.5 mg/L on September 11, 1957. This value was slightly greater than that on August 19, 1957 (Fig. 1). It is interesting that although this notch was present in 1913 and showed slightly in the detailed samples of 1933 (Robinson 1938), it seems to have also been increasing in magnitude in recent years. There is little doubt that this minimum is due to the shelf. Despite its periodic disappearance, when found it is almost always at the same depth, suggesting that the causal agent is fixed. The chemical data which will be discussed later, also leave little room for doubt.

The existence of this minimum provides an interesting demonstration of hypolimnetic water movements, since the major shelf areas are about 6 and 7 miles respectively on either side of the sampling station. A smaller shelf is present about 2.5 miles distant.

The only remaining explanation of the metalimnetic minimum is that of removal of the oxygen *in situ*. Two possibilities must be considered; first, "chemical" oxidation entailing abiotic, non-enzymatic processes; second, biological oxidation which is probably dependent on the presence of living organisms since free enzymes have not yet been demonstrated in lakes.

TABLE 1. *Oxygen (in mg/L) used up in bottles of lake water from 2 depths stored in the dark at room temperature*

Elapsed time in days	11 m		30 m	
	Untreated	Poisoned	Untreated	Poisoned
8	1.08	0.27	2.23	0.06
15	2.41	0.75	2.65	3.52
27	3.43	0.67	3.14	2.51

The importance of the "chemical" process does not seem to have been adequately established (Hutchinson 1957) and the few speculations that do exist have been confined to humic waters. Therefore, a few exploratory experiments were performed to determine the possible significance of such oxidation in Lake Washington, which is not particularly highly colored. On July 9, 1958 water was collected in a polyethylene container from 11 m (in the notch) and 30 m. For each depth, three sets of 250 ml Pyrex bottles were set up, each set in triplicate. One bottle of each set was used to measure the initial oxygen concentration, the second bottle was left untreated, and the third had about 0.5 ml of saturated mercuric chloride added to kill the organisms and inactivate their enzymes. The bottles were then placed in the dark at about 25°C. After appropriate intervals, the two bottles remaining in each set were analyzed for oxygen by the Winkler method (Table 1). Experiments showed that the amount of $HgCl_2$ added had no significant effect on the oxygen determination.

For some unknown reason the poisoned bottles in the 30-m series yielded unrealistic results which must be discounted. The 11-m results were at least reasonable and showed that the respiration in the poisoned bottles was probably about ⅕ to ⅓ of that in the unpoisoned ones. Enclosing the water in the bottles may have increased the bacterial respiration, and, if this is taken into

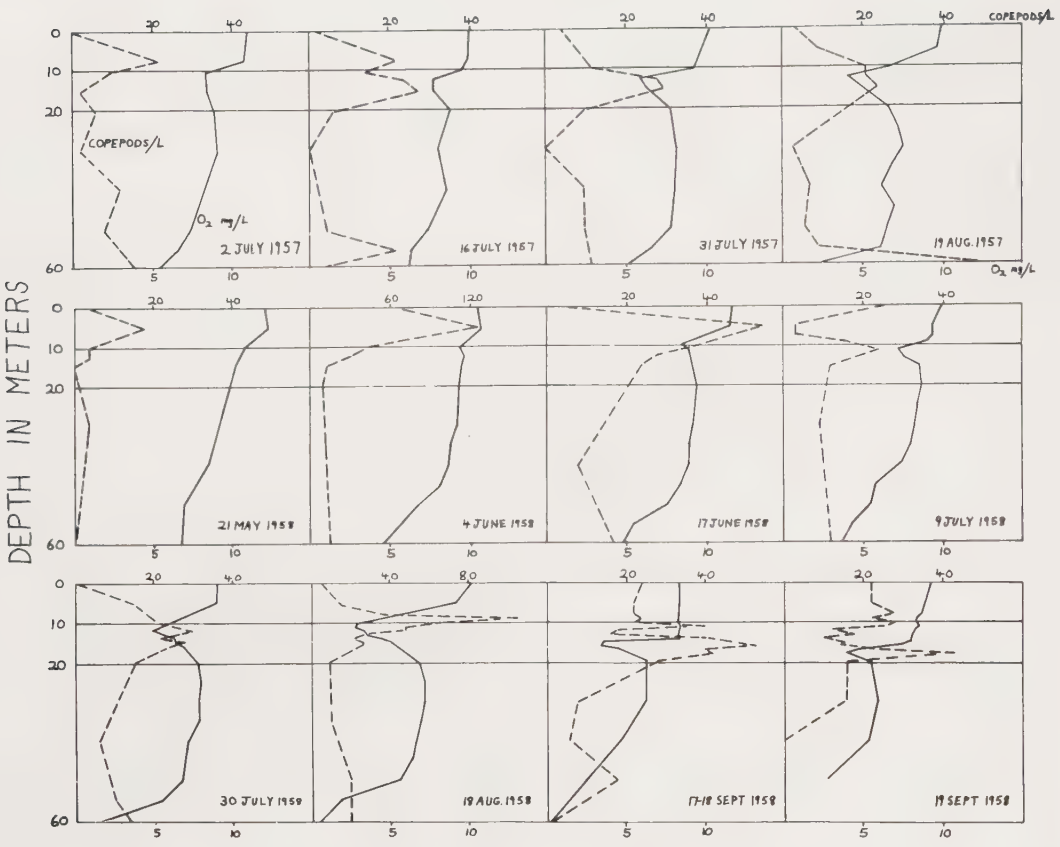

FIG. 3. Dissolved oxygen and copepods in Lake Washington during 1957 and 1958.

account, the percentage of the respiration due to "chemical oxidation" becomes higher. Offsetting this is the fact that mercuric chloride probably does not stop all biological uptake of oxygen. Therefore, the figure of 20–30% may perhaps be taken as an approximation of the true value of oxidation due to "chemical" agencies. This leaves most of the oxygen uptake still to be accounted for.

The possibility of biological oxidation resolves itself into three parts: respiration by bacteria, by algae, and by animals. Bacterial oxidation of methane (Ohle 1958) is unlikely to have been of significance in causing the metalimnetic oxygen minimum in Lake Washington since no evidence of massive formation of this gas has ever been observed in the lake, even in sediment cores taken in late summer.

The work of Kusnetzow and Karsinkin (1931) on bacteria has already been mentioned. As one of the routine determinations in studying Lake Washington, measured volumes of water collected from different depths were filtered with Millipore filters for the estimation of total seston. The difficulties which Kusnetzow and Karsinkin must have encountered were well appreciated when an attempt was made to count directly the bacteria on these filters. Although the attempt was a failure, it led to the discovery that the filters representing the region of the oxygen notch contained unusually large numbers of copepods. In subsequent work it was noted that the vast majority were alive. The results are given in Figure 3. Admittedly, 500 ml (and in a few cases 335 ml) is a small sample, but the results show no great variation and are probably sufficiently accurate for the purpose. Until the middle of July, the largest

TABLE 2. *Data showing calculation of use of oxygen by copepods in the metalimnion of Lake Washington*

Date	O_2 in minimum mg/L	Depth m	Number of copepods/L	Temp.	Δ O_2	Δ days	Mean number of copepods	Mean temp. °C	Total possible loss due to copepods mg/L	% loss due to copepods
					1957					
June 17	9.38	15	12	8.7						
					1.08	15	11	11.5	.249	23
July 2	8.30	10	10	14.3						
					0.46	14	19	12.1	.430	93
July 16	7.84	15	28	9.8						
					1.81	15	28	13.4	.646	36
July 31	6.03	12.5	28	17.0						
					1.89	19	25	16.8	1.026	54
Aug. 19	4.14	12.5	21	16.5						
					1958					
May 21 (no minimum)	10.76	10	4	11.5						
					1.46	13	25	11.4	.500	34
June 4	9.30	10	45	11.3						
					0.92	13	42	12.1	.884	96
June 17	8.38	10	38	12.8						
					1.16	22	31	12.9	1.166	101
July 9	7.22	11	24	13.0						
					2.26	21	27	15.3	1.122	50
July 30	4.96	12	30	17.5						
					2.06	19	39	17.8	1.674	81
Aug. 18	2.90	11	48	18.0						
Sept. 10	4.04	12.5	42	18.5						
					0.63	6.5	48	17.5	.695	110
Sept. 17 (midnight)	3.41	16	54	16.5						

concentrations of copepods were found above 10 m. Then, the population maximum shifted downward into the metalimnion and became associated with the already developing oxygen notch. In most cases, the coincidence of maximum concentration of copepods with minimum concentration of dissolved oxygen was very good.

Here then is a possible explanation for the oxygen notch if it can be shown that the copepods are capable of using enough oxygen. No adequate measurements of the actual respiration of the copepods were made and so the calculations were based on respiratory rates of *Diaptomus graciloides* (average of male and female) as determined by Scherbakoff (1935). The most abundant copepod in Lake Washington is *Diaptomus ashlandi,* and presumably these represented the bulk of the copepods on the filters. Identification was difficult in the dried condition. Scherbakoff gives the mean lengths of *D. graciloides* as: female 1.24 mm; male 1.14 mm. Wilson (1959) gives ranges for *D. ashlandi* of: female 0.93–1.4 mm; male 0.9–1.2 mm. All of these figures are presumably total lengths, as the metasomal lengths of *D. ashlandi* in Lake Washington are: female 0.81–0.98 mm; male 0.71–0.82 mm (Comita 1955). According to Comita the animals reach their maximum size early in July and their minimum size late in October in Lake Washington.

Assuming that all of the copepods were alive and of about the same size as *D. graciloides,* in most cases they would have been able to use up a considerable amount of the oxygen lost from the notch (see Table 2). (Calculations using the limited data of Vollenweider and Ravera (1958) for *Mixodiaptomus laciniatus* yield very similar results. Wilson gives the size range of the subgenus as: female 1.5–2.0 mm; male 1.4–1.6 mm). This assumes, however, that the copepods spent 24 hours a day in the

oxygen depleted layer. Some estimate of the effect of the diurnal migration is, therefore, necessary. In Figure 3, the curves for September 17–18, 1958, were plotted from samples taken at midnight, and those for September 19, 1958, from samples taken at noon when the sky was clear. On both occasions a copepod maximum coincided with the oxygen minimum. The depression of the oxygen minimum and copepod maximum to a slightly lower depth on September 19 may be connected with high winds during the previous day.

Therefore, it seems reasonable to attribute the metalimnetic oxygen notch in Lake Washington largely to copepod respiration. Scherbakoff, however, concluded that the crustacea in Lake Beloje could account for only 2.5–6% of the total oxygen used. Since his calculations show that they could have used 0.1 mg/L/24 hrs in summer, and 0.01 mg/L/24 hrs in winter, he must have been referring to respiration in the epilimnion, since such total rates in the hypolimnion would cause it to become anaerobic in a few days. In this regard, it is interesting that Vollenweider and Ravera found that the crustacea in Lago Maggiore were capable of using between ⅛ and ⅓ of the oxygen produced by photosynthesis. The difference between the two lakes is probably due to the fact that Lake Beloje is much more eutrophic than Lago Maggiore.

In Lake Washington the copepods are accompanied by other animals and by bacteria and sedimenting phytoplankton which would also use up oxygen. Since the lake has a low transparency (Secchi disc in summer = 1.5–3.2 m), any phytoplankton falling through the metalimnion would be respiring without any compensating photosynthetic production of oxygen. It might appear, therefore, that the estimate of the proportion of the oxygen consumed by the copepods is too high. There are, however, two facts which suggest that bacterial and phytoplankton respiration are of secondary importance in the notch region. The first is the difference in response to bottling of water from 11 m and water from 30 m (Table 1). During the first 21 days of the experiment the oxygen concentration in the 11-m bottles (25°C) fell by about 3 mg/L. The loss in the lake at 11 m (19°C) during the corresponding period was 2.17 mg/L. Similarly, the 30-m bottles (25°C) lost about 3 mg/L compared with 0.40 mg/L in the lake at 30 m (9°C). Thus, even when allowance is made for the higher temperatures in the bottles than *in situ*, it is clear that bottling had a greater effect in increasing the respiration of the 30-m water than the 11-m water. This would suggest that the bacteria in the 30-m samples multiplied rapidly while the bacterial population in the 11-m bottles remained relatively static. Since the copepod counts at the 11- and 30-m levels were 24 and 9 per liter respectively, one could speculate that the presence of the higher concentrations of copepods limited the normal response of the bacteria to the increased surface afforded by the bottle wall. This may have been brought about by grazing or by an antibiotic action.

The second reason for believing that the copepods are of prime importance is that the total seston values frequently lay on a smooth curve through the notch region. There was no evidence of the slight maximum which would be expected on the basis of the numbers of copepods, whose weight would be added to that of any bacteria and phytoplankton present. Possibly the copepods were consuming bacteria and phytoplankton and converting part of them into soluble, and in this case unmeasured, form.

The similarity of the 27-day BOD values (Table 1) in the 11- and 30-m samples also supports the suggestion that no maximum of organic matter was present in the notch. Recently, Stangenberg (1959), using the BOD method, has come to the same conclusion regarding the Polish and Italian lakes which he studied.

The increase of the notch over the past years is probably due to the increase in the numbers of copepods resulting from the sewage enrichment of the lake. For example, in May and June of 1957 the average epilimnetic population of copepods was about 6 times as large as in 1950. Indeed, there is some evidence even from the figures in Table 2 that the greater rate of oxygen

TABLE 3. *Relationships of various chemical properties to the two minima of dissolved oxygen in Lake Washington. Maxima and minima are defined as concentrations greater or lesser, respectively, than the concentrations measured immediately above and below. The numbers are the number of times a given relationship has been observed. "In min." means that the maximum or minimum of the given property corresponded exactly with the depth of lowest oxygen concentration in the notch. "Above min." and "below min." mean that the correspondence was not exact. "Above" and "below" indicate a distance of 5 m or less.*

Property	Metalimnetic oxygen minimum	Hypolimnetic oxygen minimum
pH	0	0
Si	0	1 max. in min.
HCO_3^-	1 max. in min.	0
Chlorophyll[1]	Frequent max. above min.	0
Total Seston[2]	3 min. 2 m below min. 2 max. before min. formed*	0
Free CO_2	6 max. in min. 3 max. below min.	4 max. in min.
Diss. N[3]	3 max. in min.	3 max. in min.
NH_3	0	0
NO_3	1 max. above min. 1 max. in min. 3 max. below min.	4 max. in min.
NO_2	1 max. in min.	0
Total P.[4]	8 min. below min. 2 min. in min. 1 min. before min. formed*	4 max. in min.
Diss. P.[4]	2 max. in min.	4 max. in min.
PO_4–P	1 max. in min. 2 max. below min. 1 min. below min.	10 max. in min. 2 max. below min.

* May 21, 1958.

[1] Measured by extraction, with 90% acetone, of the plankton retained on S & S #576 filter paper.

[2] Measured after filtering and drying (80°C) on tared type HA Millipore filters (0.45μ pore diameter). A blank correction was made for the loss of weight of the filter caused by passing water through it. Although this is an excellent way of determining seston, the filters when being weighed must be entirely on the balance pan or their electrostatic attraction to the floor of the balance will cause large errors.

[3] Determined by the Kjeldahl method on water passed through a Millipore filter.

[4] Determined by wet oxidation with perchloric acid, the former on raw water and the latter on Millipore-filtered samples.

depletion in the notch in 1958, than in 1957, was paralleled by a larger concentration of copepods.

As noted earlier, Lake Washington has a "morphometric" notch at 40 m. In order to compare its properties with the copepod-generated minimum, the available data from 1933 through 1958 has been summarized in Table 3. Since samples between 10 and 20 m. depth often were taken at 1 m intervals, while 5 m was the closest interval used for the deeper notch, exact coincidences of depth are more meaningful in the former case. It should be noted that on no one date were all of the listed features exhibited simultaneously. It is possible that this would not have been the case with closer sampling.

The results for seston are particularly interesting because, as noted above, they provide some support for the idea that the loss of oxygen in the metalimnetic notch is mainly due to copepods. On the two occasions on which there were maxima of total seston at 12.5 m, no oxygen minimum was present. Just earlier, the spring bloom

had begun to decline and presumably the increase in falling seston was a reflection of this. Counts of copepods on these dates, May 14 and 21, 1958, showed the bulk of the animals at about 5 m while few were found at 12.5 m (Fig. 3). The suggestion is that the maximum of non-copepod seston at 12.5 m was able to persist because there were few copepods at that depth. During the summer when the copepod maximum lay in the metalimnion, the absence of a maximum of total seston suggests solubilization of this non-copepod seston by the copepods.

One point which is difficult to reconcile is the minimum of total phosphorus which coincided with the seston maximum on May 21, 1958. This may be due to a technical error. More reasonable was the frequently observed coincidence between a minimum of total seston and a minimum of total phosphorus. However, the reason that these minima occurred below the oxygen notch is not clear. The phenomenon may reflect the fact that if the copepods above have eaten and converted much of the falling material to soluble form it can no longer fall. In this case the increase in seston farther down must be considered due to bacteria. An alternate and perhaps better explanation could be based on the assumption that a given quantity of mixed zoo- and phytoplankton would fall through the water more quickly when compressed into a single fecal pellet than as discrete particles. Thus, material eaten by the copepods in the region of the notch would fall relatively quickly through the next few meters. Then as the fecal pellets began to loosen, their descent would be slowed.

The maximum of chlorophyll, frequently present just above the notch, is reminiscent of the large mass of bluegreen algae which Thomas (1958) found similarly located in the Zürichsee. Lake Washington is now dominated by such algae and the high chlorophyll values undoubtedly indicate the same situation as in the Swiss lake. It is unlikely that the respiration of these algae contributes substantially to the loss of oxygen from the notch since the oxygen values at their level are relatively high compared to those found a few meters lower.

The CO_2 data provide an interesting comparison between the two notches, for if the free CO_2 anomaly (see Hutchinson 1958 p. 679) is calculated for various strata between June 17, and September 11, 1957, the values are:

10–20 m	− 4.8
20–30 m	+16.2
35–45 m	+18.5
50–60 m	+ 7.4

Although these values because of technical difficulties with reagents are possibly not correct in the absolute sense, they are mutually comparable and they show that much of the CO_2 produced in the hypolimnetic notch arises from a different source than that in the metalimnetic notch. Probably the difference is due to anaerobic respiration in the mud of the deep shelf for, as Hutchinson points out, such positive values are strongly indicative of anaerobic respiration. (In the discussion on page 679 of Hutchinson, the sixth line in the paragraph headed "The CO_2 anomaly..." should read "free CO_2 anomaly.")

It is not too surprising that the pH shows no minima corresponding to CO_2 maxima. Although the instrument used to measure pH (Beckman, Model G) was sufficiently sensitive to detect such small variations, the method of collecting the samples probably affected the results; while the samples for CO_2 measurements were taken in the small filled glass bottles later used for the titration, the pH was measured after the water had been returned to the laboratory in large plastic bottles. Thus any excess of CO_2 would probably have been dissipated causing the pH to rise.

The PO_4 and NO_3 data taken together provide another good reason for relegating bacteria to a secondary role in the consumption of oxygen in the metalimnion. In part, bacteria decompose substances by releasing enzymes extracellularly. Thus, if bacteria were to decompose some falling seston, the PO_4 and NO_3 formed would be present in the water and would coincide with any oxygen minimum that might be associated with bacterial respiration. However, if cope-

pods were mainly responsible for the decomposition (digestion), the substances formed would be expelled in fecal pellets and would not be set free until the pellets had sunk somewhat deeper. This is exactly what seems to be happening with the PO_4 and NO_3. Riley (1951) has described a similar situation in the ocean.

The nitrate and phosphate data, along with those for total phosphorus, also provide strong evidence for different causes of the two oxygen minima. The behavior of these substances in the lower notch conforms to the idea that the oxygen is taken up at a mud surface which in turn releases soluble substances into the same stratum. No analogous explanation is possible for their distribution in the metalimnetic layer. However, even in the absence of a shelf in the upper notch region, large amounts of dissolved substances could be suddenly released into the notch if the oxygen concentration were to fall sufficiently low. It is anticipated that this will happen within the next few years.

One further point about the lower notch is that it seems to occur at about 40 m while the shelf is between 30 and 35 m. Presumably, this is because the water with its load of solutes is slightly denser than the water above and below in spite of the slight temperature differences which must exist, but which cannot be seen on bathythermograph traces. Investigation of this "sinking" effect was proposed for 1958, but the notch was then too poorly developed probably due to the very windy summer.

RELATION TO PREVIOUS INVESTIGATIONS

While the observations of Whitney, Wood, and Miyake and Saruhashi indicate that the hypothesis of Birge and Juday may have some validity no such evidence has been gathered from this investigation. In fact, on only two dates were maxima of seston observed in the metalimnion. These followed the collapse of a large bloom and no oxygen minima were associated with these maxima. Rather, the data presented here indicate strongly that the metalimnetic oxygen minimum in Lake Washington is caused largely by copepod respiration and thus support Minder's view.

Earlier, Naber (1933) had concluded that it is unlikely that (freshwater) zooplankton can cause irregularities in the oxygen curve. He determined the respiratory rate of *Cyclops strenuus* and calculated, using earlier data of Minder, how many entomostraca were required for the known loss of oxygen from the hypolimnion of the Zürichsee. In each case the calculated numbers of entomostraca exceeded those found by Minder. However it should be noted that while Naber reported a mean length for *Cyclops strenuus* of 1.13 mm, the (♀) *Cyclops strenuus* used by Scherbakoff (1935) had a mean length of 2.31 mm. (Wilson (1959) gives size ranges for this species of: ♀ 1.42–2.35 mm; ♂ 1.28–1.56 mm.) This difference in size leads to a large difference in respiratory rate, each of Naber's animals using only 1.26 γ O_2/24 hrs (19°C) compared to 6.97 γ O_2/24 hrs (20°C) used by Scherbakoff's *C. strenuus*. This figure of 1.26 γ O_2/24 hrs exceeded those found by Scherbakoff, for various species, only in the case of ♂ *Cyclops leuckarti* which were 0.75 mm long and respired 0.41 γ O_2/24 hrs at 20°C. The other figures given by Scherbakoff are:

Diaptomus graciloides, ♂ 1.14 mm, 2.29 γ O_2/24 hrs;
Diaptomus graciloides, ♀ 1.24 mm, 2.84 γ O_2/24 hrs;
Cyclops leuckarti, ♀ 1.00 mm, 1.48 γ O_2/24 hrs;
Daphnia longispina, ♀ 1.64 mm, 5.36 γ O_2/24 hrs.

Another objection to Naber's conclusion may be found in his example of the Schöhsee. Using his own data for this lake he calculated that the entomostraca and rotifers present in the 24–27 m stratum could have used only about ⅓ of the oxygen lost during a 32 day period of observation. However, to judge from his Figure 10 the lake is only about 27–28 m deep and it is therefore reasonable to assume that much of the oxygen lost between 24 and 27 m was used up by processes associated with the

bottom. Finally, although he believed that zooplankton cannot appreciably influence the shape of the oxygen curve, in at least one of his figures a definite maximum of zooplankton coincides with a metalimnetic minimum of dissolved oxygen.

Bacteria which Kusnetzow and Karsinkin showed to be of importance in Lake Glubokoje appear to be of minor significance in Lake Washington. This is perhaps why phosphate maxima were uncommon, since Riley (1951) has noted that the O/P ratio for zooplankton is probably higher than that for bacteria.

Winberg (1934) pointed out that, in a lake in which the metalimnion is below the compensation point, an oxygen notch is likely to develop in the upper part of the metalimnion due to the temperature characteristics of this region. No matter what the agency, whether oxygen consumption is chemical, or due to bacteria, phytoplankton, zooplankton, or a shelf effect, it will necessarily proceed at a faster rate in the upper warmer region than below. Also, it is to be expected that the amounts of substrate reaching the lower part of the metalimnion will be reduced and probably more refractory. Considering this it is difficult to contemplate a lake of suitable transparency in which there is no metalimnetic minimum. It is, therefore, suggested that the apparent absence of a minimum may often be an artifact due to insufficiently close sampling with depth.

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NOTES AND COMMENT

Differential Titration with Strong Acids or Bases vs. CO_2 Water for Productivity Studies

In the October 1959 issue of Limnology and Oceanography Beyers and Odum present curves contrasting differential titrations of natural waters using H_2SO_4 and H_2CO_3 solutions. They show a marked divergence of the curves so obtained and suggest that CO_2 changes computed from differential titrations with strong acids or bases are too low. They have, however, made an error which invalidates their argument. They failed to take account of the fact that a molecule of H_2SO_4 reacts with bicarbonate to produce 2 molecules of H_2CO_3, hence the addition of one mole of H_2SO_4 is equivalent to the addition of 2 moles of H_2CO_3. If one takes account of this discrepancy, then their curves coincide in the early part of their range. Usually, in natural waters, one is interested in a relatively small portion of the curve (pH 8–9, or 7–8) and such a portion of the curve can be examined conveniently, and accurately, by simply bubbling respired air through the natural water to bring its pH to the desired starting point, then performing the differential titration with 0.02N NaOH. Each ml of this solution will absorb 20 micromoles of H_2CO_3 from solution, or, at higher pH, will convert 20 micromoles of bicarbonate to carbonate, in close analogy to the changes produced by photosynthesis. The addition of NaOH will, of course, alter the total alkalinity slightly, but this influence is small when examining the limited region of the pH curve usually required in a study under natural conditions. The titrations with CO_2 water, described by Beyers and Odum, provide reliable curves, but the titration with 0.02N NaOH is much more simple and convenient, and is equally reliable in every natural water that I have encountered. Beyers and Odum do not refer to the work of Moberg *et al.* (1934) in which they show that differential titration curves in sea water agreed closely with total CO_2 determinations via the Van Slyke apparatus. Neither did they understand my (1956) comparison of differential titration curves with the curves computed from Dye's nomograms or they would have noted that my differential titration curves yield higher CO_2 changes than are computed from Dye's nomograms. Frey and Stahl (1958) also observed a discrepancy in this direction. Beyers and Odum leave the erroneous impression that Dye's nomograms are more reliable than differential titrations with NaOH in fresh water. This is not the case. On the contrary, differential titration with NaOH is the method of choice for relating pH change to CO_2 change in productivity studies because it avoids the problems associated with the handling of H_2CO_3 solutions.

In the graph presented by Beyers and Odum below, the HCl curve agrees closely with the CO_2 curve between 8.7–7.5 which is in contrast to their previously published curve (Beyers and Odum 1959). This is the point I wish to make. When a differential titration with HCl or NaOH is extended over more than one pH unit, slope deviations become important.

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Verduin (1960) believes that adding one molecule of NaOH has the same effect on the bicarbonate equilibrium as withdrawing one molecule of H_2CO_3 (as by a plant in

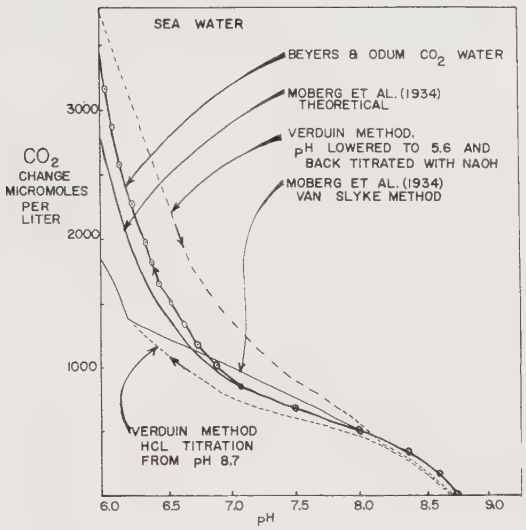

FIG. 1

photosynthesis). His contention is wrong theoretically and experimentally. To convert the previously published graphs (Beyers and Odum 1959) into the form recommended by Verduin, one simply multiplies the H_2SO_4 molarity by 2. The H_2SO_4 and H_2CO_3 curves still do not agree.

The effects are different since the equilibria are shifted in a different manner. The error of his method of computation is not a constant factor but varies markedly with pH. The error is small at pH 8.5 and very large at pH 7.5. For computing metabolism from observed changes in pH it is the slope that is important.

Verduin writes a stoichometric formula with exactly one mole of H_2CO_3 equivalent to a mole of HCl or NaOH step by step in the titration. One cannot do this. The only way to convert a titration with a strong acid or base into a curve of total CO_2 and pH is to titrate to completion to get alkalinity and then calculate the total CO_2 for each state of equilibrium as conveniently described in textbooks by Sverdrup and Harvey.

Verduin apparently misunderstood Moberg, Greenberg, Revelle, and Allen (1934), believing that these authors had reported stepwise titrations with strong acid. Moberg *et al.*, changed the total CO_2 content stepwise by adding or withdrawing CO_2 by passing CO_2 or CO_2 free air through sea water. Then they plotted points on a graph of total CO_2 and pH (colorimetrically) with points determined in three ways, with only fair agreement:

A. Total CO_2 was determined with the Van Slyke method (See Fig. 1).
B. Total CO_2 was computed from equilibrium constants (See Fig. 1).
C. Total CO_2 was computed from the sum of methyl orange alkalinity and phenolpthalein alkalinity. This line was similar to the Van Slyke method.

They did not, however, report a stepwise titration curve of pH versus strong acid or base.

In the Figure 1 we have titrated sea water with CO_2 water as previously described and plotted moles as a function of pH observed.

For comparison, the theoretical curve from equilibrium constants by Moberg *et al.* is plotted. The agreement with the curve from CO_2 water is better than with these authors' own experimental data with the Van Slyke method and colorimetric pH methods. Also in the Figure 1 we have plotted a titration of pH with HCl on the same water and have computed according to Verduin's instructions (one mole CO_2 as equivalent to one mole HCl). In both graphs correction is made for dilution so that the molar concentrations refer to the actual concentration in the titration vessel at all times. The curves are different in slope.

Verduin indicates that sometimes he lowers the pH with CO_2 and back titrates with NaOH. This procedure we have tried on the same water. It gives still another curve not consistent in slope with Verduin's acid curve (See Fig. 1).

Beyers has improved the CO_2 titration method for routine use with a special burette with a magnetic stirring capsule for equilibrating CO_2 over a flat gas-water interface in a swollen upper portion. He has over a hundred 24-hour recordings of balanced aquarium metabolism with a Beckman zeromatic pH meter and Honeywell recorder.

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Light and Dark Bottle Experiments in Alaska

In the course of an investigation, during the summer of 1958, into the effect of the Katmai ashfall on the trophic status of two lakes in the Kodiak region, Alaska, measurements of primary production were made.[1] Both lakes have surface areas of about 45 ha, maximum depths of about 29 m, and are located within 2 miles of each other on Afognak Island.

The "light and dark" bottle technique of Gaarder and Gran (1927) was used although the low sensitivity of the method renders it marginal for use on oligotrophic lakes. Frey and Stahl (1958) were able to use it successfully, however, on several arctic lakes. Dissolved oxygen concentrations were determined by the un-modified Winkler method. The length of exposure was usually 24 hours, rarely extended to 48 hours. We first made certain that it was possible to fill three BOD bottles from the same sample of lake water contained in a Kemmerer bottle, fix them and, upon subsequent titration, obtain identical results for each (within the limits of the experimental error). The Kemmerer bottle was not coated with plastic or wax, but had been in use for a number of years. The use of the same kind of sampler did not appear to affect the results obtained by Frey and Stahl (*ibid.*).

Satisfactory results were obtained from our early experiments, *e.g.* in mid-July gross photosynthetic rates of 25–50 μg C/L/day were measured. From then on, a situation developed in which the bottle exposed to light contained less oxygen than the dark bottle at the end of the experiment. The difficulty appeared first in Upper Jennifer Lake in the deeper regions and spread toward the surface. In Little Kitoi Lake the phenomenon appeared about two weeks later near the surface and spread downwards. It became nearly impossible to obtain positive indications of carbon fixation in either lake for the remainder of the summer.

Some representative data are given in Table 1. In practically every case, the dark bottle apparently contained more dissolved oxygen than the light bottle at the end of the experiment. In Little Kitoi Lake, the blank (sample taken from the same Kemmerer bottle, fixed and titrated at the beginning of the experiment) consistently showed an oxygen concentration higher than either the light or the dark bottle, while in Upper Jennifer Lake the blank ordinarily contained less than either light or dark bottle. The August 25–26 data for Upper Jennifer Lake are plotted in Figure 1.

A possible explanation for the higher oxygen concentrations in dark than in light bottles might be found in the recently discovered dependence of respiration rates of some photosynthetic organisms upon oxygen concentration (Gessner and Pannier 1958). These authors indicate that respiration rates in darkened bottles will be too low due to the lack of the locally high oxygen tensions present in light bottles. Thus it is entirely possible for calculated gross photosynthetic rates to take on negative

[1] Supported by a grant from the National Science Foundation. Laboratory facilities were provided at the Kitoi Bay Laboratory by the Alaska Department of Fish and Game.

TABLE 1. *Results of 24 hour light and dark bottle experiments on two lakes in Alaska during August, 1958*

Date	Depth meters	Little Kitoi Lake ppm Oxygen			Upper Jennifer Lake ppm Oxygen		
		Blank	Light	Dark	Blank	Light	Dark
Aug. 11–12	1	9.69	9.38	9.56	9.15	9.32	9.54
	5	9.66	9.27	9.55	9.52	9.14	9.50
	9	9.92	9.90	9.78	10.97	11.61	12.36
	10	10.09	9.84	9.88	10.96	11.53	12.17
	14	9.96	9.85	10.06	10.31	9.90	10.51
Aug. 25–26	1	9.69	9.28	9.32	8.72	9.32	9.66
	5	9.66	9.41	9.47	9.16	9.37	9.50
	9	9.64	9.29	9.17	10.96	11.53	11.53
	10	9.80	9.18	9.27	11.08	11.77	11.80
	14	9.78	9.43	9.56	9.61	10.44	10.45

values, particularly at low rates of production. In this connection it should be noted that a mistake was made in the final paragraph of Gessner and Pannier's article. The first sentence should read "Values obtained by the Winkler method for the *gross* (not *net*) rate of photosynthesis are somewhat too low." The words in italics are interchanged in the original paper). The behavior of the blanks in Upper Jennifer could not be accounted for by this phenomenon; however, the curves of Figure 1 suggest that a relatively constant loss of oxygen may have been introduced somewhere in the oxygen determination, possibly during the 10–15 min this bottle remained unfixed while the light and dark bottles were filled and lowered to the proper depth. The possibility of photo-chemical oxidation of the humic material in this lake should not be overlooked.

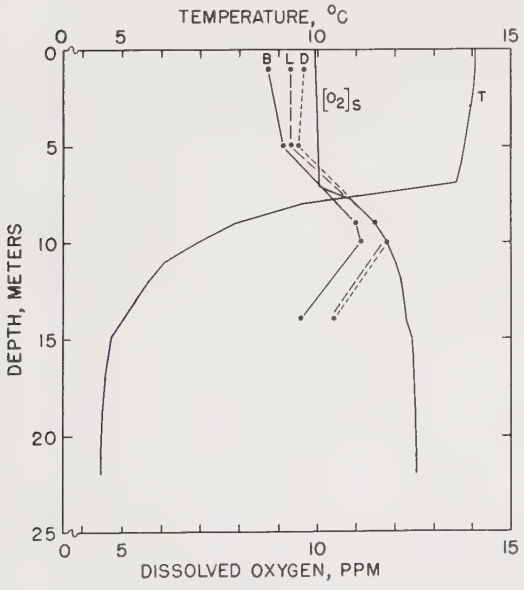

FIG. 1. Upper Jennifer Lake, August 25–26, 1958. T, temperature; B, oxygen concentration in blanks; L, oxygen concentration in light bottles; D, oxygen concentration in dark bottles; $(O_2)_s$ = oxygen saturation at observed temperature.

A similar situation was found in Lake Quassapaug, Connecticut, during the latter part of July, 1938, by Riley and Hutchinson (Hutchinson 1957, p. 616). The oxygen curves for this lake are of the same type as that of Upper Jennifer Lake (*i.e.* with a metalimnial maximum). Hutchinson suggests that a photokinetic effect on the zooplankton might be responsible for the increased oxygen depletion occurring in the light bottle.

From personal discussions we have found that many investigators have encountered a similar reversal of the final oxygen concentrations in light and dark bottle experiments but have ignored the results, attributing them to experimental errors. Our results are consistent enough to suggest that a rational explanation could probably be obtained if a thorough investigation were made.

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Procedure for and Comments on Ice Point Tests of Deep Sea Reversing Thermometers[1]

One of the most basic and important tools of the physical oceanographer is the deep-sea reversing thermometer. The soundness of theories on the behavior of the oceans, and the validity of proof supporting or refuting such theories depends, in no small part, upon the accuracy of hydrographic observations obtained by means of these instruments.

Reversing thermometers are constructed with great care and precision but a calibration of each instrument is necessary before it can be properly used.

The purpose of this calibration is to determine for each instrument: 1) the corrections necessary at each of a number of selected points along the scales of the main and auxiliary thermometers, so as to reduce the thermometer reading to actual temperature; 2) the volume of the small bulb of the main thermometer to the zero degree mark ($V_\circ$), and 3) in the case of an unprotected thermometer, the pressure factor (Q) which is needed to determine the depth of the instrument at the time of reversal.

The scale corrections are determined by comparing the readings of the main and auxiliary thermometers of each instrument with the corrected reading of a "standard" thermometer of known accuracy at a series of selected points. These points are generally not more than 50 scale divisions apart for the main thermometer, and every 10° for the auxiliary. To prove reproducibility and determine a mean or average correction at each calibration point, several successive reversals should be made at each temperature point. With proper care and equipment, the correction determined at each such calibration point on the main scale of a good instrument should be accurate to within about 0.05 of a scale division. Auxiliary corrections are usually determined only to the nearest 0.1°C.

$V_\circ$ is determined by reversing and reading the main thermometer at an accurately known temperature, changing the temperature of the reversed thermometer to another accurately known temperature, about 30–40°C different from the first reading, and then dividing the difference between the two main readings ($T''-T'$) by the actual temperature change (t) times the glass constant (k)

$$V_\circ = \frac{T'' - T'}{t \times k}$$

Several such tests should be made to determine an average value, which should be accurate to about one part in 100.

Q is determined in the laboratory by a series of reversals at accurately known pressures, 100 Kg/cm² or greater, and accurately known temperatures, generally at or near 0°C. The corrected reading of the unprotected thermometer (T_u), less the actual temperature (T_w), divided by the pressure in Kg/cm² gives the pressure factor

$$Q = \frac{T_u - T_w}{P}$$

A number of such tests at different pressures should be made to determine an average for each depth (pressure) and to determine linearity of pressure response. Q should be accurate to about one or two meters per thousand.

All of this calibration procedure is exacting, time-consuming, and requires a rather extensive and elaborate array of equipment to attain the desired degree of accuracy; it is therefore also relatively expensive, from 20% to 40% of the cost price of the instrument, depending upon the type and range. Without such calibration, however, the instrument is relatively valueless to the oceanographer.

Once such calibration has been accomplished, certain characteristics of the instrument are known and fixed. Barring the necessity for major glass repairs or the opening or changing by heat of the dimensions of the main capillary system, $V_\circ$ and the relation of the established scale corrections,

[1] Contribution No. 1064 from the Woods Hole Oceanographic Institution.

one to another, will not change. Many laboratory rechecks of Q indicate that this value does not change with age or use within the pressure endurance capabilities of the instrument.

The ice point (reading at 0°C) can, and generally does, change with age. The amount of such change, the rapidity with which it may occur, and the period of time during which change may continue will vary greatly from one instrument to another. The direction of such change is most often in the direction of higher readings but may be downward, and may even be first in one direction and later in the other. There are two principal factors involved in such change; the shrinkage, with age, of the glass of the thermometer bulb, and in the case of a protected thermometer the gradual diffusion of a superatmospheric pressure around the bulb, initially created by the driving down of the cork plug during assembly.

Proper artificial "ageing" of the thermometer glass in the course of manufacture of the instrument minimizes the subsequent bulb shrinkage and consequent upward zero point shift resulting from natural ageing. It is possible to relieve any excess pressure below the cork plug by venting the area below the plug with a fine hypodermic needle. When these things have been done, the zero point shift with age is generally very slight, and may not become apparent for a year or more, and after two or three years the zero reading will, in most cases, have become stabilized. Where the bulb has not been artifically "aged," or when superatmospheric pressure exists around the bulb, the zero point may shift slowly but continuously for years.

It is always possible that there may exist in the bulb unrelieved stress just below the relief threshold. In such case, a severe jar or vibration, or exposure to extremes of temperature may cause ice point shift. It is probable that most ice point shifts resulting from bulb shrinkage are quite sudden, a shift from one level to another occurring at some particular moment in time, the ice point then remaining stable for a period until the stress relief threshold may once again be reached.

If he wants accurate data, the oceanographer must see that the accuracy of the original calibration is verified from time to time and that proper adjustment of the scale corrections are made in the event of ice point shift. If the ice point reading (and hence correction) changes, the corrections determined at all other points on the thermometer scale will change in the same direction by the same amount.

It is recommended that all reversing thermometers should be given an ice point check not more than six months after the time of initial calibration, and then rechecked every six months until the ice point appears to have become essentially stabilized. Thereafter an ice point check perhaps once a year is desirable. An ice point check should always be made after the thermometer has undergone any factory repairs, major or minor.

While all calibration laboratories can and do perform these checks, such tests are somewhat expensive, and there is the risk to the thermometers of damage or breakage during transportation to and from the testing laboratory.

The method for checking the ice point is relatively simple and can be undertaken by any organization using reversing thermometers as follows:

A. *Requirements*

1. Finely crushed fresh water ice must be used. (100% through 1″ square screen; 50% through ½″ square screen.)
2. Ice must be physically clean and chemically free from any dissolved substance that might lower the melting point. Most good commercial ice satisfies this requirement, and distilled water ice generally need not be used. (The melting point of distilled water ice at atmospheric pressure is 0.000°C. While a depression of a few thousandths of a degree may occur in essentially "clean" commercial ice, this is generally not significant. How-

ever, commercial ice that is chemically or physically impure may have a melting point down to several hundreths of a degree below 0.000°C. A check on the purity, and hence the "accuracy," of the ice should be made by including in each group of thermometers tested a thoroughly reliable protected reversing thermometer, the ice point of which is known and has become stable. It is perhaps desirable to have more than one of these so-called "standard" or "check" thermometers, the ice points of which can be verified by the use of distilled water ice in the procedure described below.)

3. Ice must be in melting condition. Melting can be promoted by sprinkling with distilled water.
4. The thermometers must be entirely free from any trace of salt. Rinse well in fresh water before test series.

B. *Procedure*

1. Thermometers are placed upright in ice in a container about 18″ deep. The container should have drainage in the bottom. If the container is insulated the thermometers should be not closer than 1″ to the sides; if uninsulated they should be not closer than 2″ to the sides. The lower ends of the thermometers should be not closer than 3″ to the bottom of the vessel. There should be not less than 3″ of ice over the top of the thermometers, and this should be covered to prevent air circulation.
2. The thermometers should stand in the ice for approximately one hour, after which each thermometer in turn should be carefully and quickly uncovered enough to permit the grasping of the upper end. The thermometer is then quickly withdrawn from the ice, instantly reversed, returned to the hole in the ice from which it was withdrawn, and recovered with ice.
3. When all the thermometers have been thus reversed, they should be allowed to stand about 15 minutes to ensure that all parts of the instrument, internally and externally, have lost the small amount of heat absorbed in the process of reversal and have returned to a temperature of 0.00°C.
4. Each reversed thermometer in turn should then be carefully uncovered enough to permit grasping its upper end. The thermometer is then quickly withdrawn from the ice only far enough to make visible the top of the mercury column of the auxiliary. Using a viewer or loupe of about 5× magnification, first the auxiliary, and then, withdrawing the instrument further, the main thermometer is read. This should be done as quickly as possible in order to avoid the effect of the ambient temperature. The time from the beginning of withdrawal of the thermometer until completion of both readings should be not more than 10 seconds. During all of this operation the extreme lower end of the reversed thermometer should remain surrounded by ice.
5. Care should be taken to avoid error due to parallax. A mask on the eyepiece with an orifice of about 3/16″ diameter centered on the optical axis is extremely helpful in this regard. A tube or other stand-off device on the objective end of the viewer, which can be placed against the outside of the thermometer shell to maintain the proper focus of the image, is also helpful.
6. In humid weather, fogging on the outside of the thermometer shells can be controlled by wiping a slight film of substance such as saddle soap on the shells in the vicinity of the zero points. Internal fogging of unprotected thermometer shells and stems can be controlled by rinsing the inside of the instruments with a little liquid detergent solution prior to placing the instruments in the ice.
7. It is preferable to pre-chill the reservoir ends of the thermometers

prior to each test by standing them upright in about 6″ of clean ice mixed with water for a few minutes. This ensures that the reservoir end will not melt an air space around itself.

8. If a double-ended ice vessel with removable end caps is provided for the tests, after the thermometers have stood for one hour in the ice, the entire vessel can be reversed, thus reversing all the thermometers at once and eliminating the necessity for the steps outlined in paragraphs 2 and 3.
9. It is not safe to determine the ice point correction of the main thermometer based on one test (reversal) only. At least two tests should be made, and if these do not agree, a third test should be made and an average taken to determine the main ice point correction. If readings are several hundredths of a degree apart, additional tests should be made until a good average can be obtained, discarding readings which are apparently aberrant. The only condition under which one reversal is adequate would be when it agreed with the ice point reading previously determined in a proper manner, in which case it is safe to assume that no change in the ice point has occurred since the last determination. One reading of the auxiliary is generally satisfactory, as the correction is normally stated only to the nearest 0.1°C.

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Home-made Counting Chambers for the Inverted Microscope

In the course of an investigation of the vertical distribution of flagellates in the Sargasso Sea, an improvement in method was made by the author, which may prove valuable to other workers on phytoplankton. The inverted microscope (Utermöhl 1930) was chosen for this investigation because its use provides the simplest and quickest method for the enumeration and identification of the phytoplankton in a known volume of water.

In spite of Braarud's (1954) recommendation that counting methods be standardized, particularly with respect to the volume of water to be sampled, the writer feels that the standardization should rather define the number of organisms to be counted (Holmes and Widrig 1956; APHA 1955). To achieve this, it is desirable to have available an assortment of counting chambers. The proportions of the cylindrical counting chambers used on the inverted microscope have no effect on the theoretical efficiency of this method, but they turn out to be of considerable practical importance. A dense population is most easily counted in a squat cylinder, that is, one in which the bottom area is large relative to the volume. In a squat cylinder, the organisms have a relatively large area to settle out on and do not pile up into heaps which would hide some of them. However, a sparse population is best counted in a tall, narrow cylinder, in which the bottom area is small relative to the volume, because the time it takes to count a given sample is in part dependent on the area to be scanned. (This became obvious to the writer when he discovered that it was requiring as much time to examine the extremely sparse Sargasso plankton as it had to count populations ten thousand-fold more dense.) A cylinder height of more than about 1.5 cm, however, precludes the use of a condenser on the inverted microscope. This has the effect of making everything fuzzy, rendering identification difficult and thereby again greatly increasing counting time. Accordingly, bipartite cylinders with removable upper parts were used.

The expense of obtaining a wide assortment of counting chambers can be avoided by making one's own. Glass tubing, of the appropriate diameter, is sawed to the appropriate length. The cut edges are lapped smooth with carborundum powder in water on a glass plate. The bottom of the cylinder is painted lightly with rubber cement (any one of the several brands of the new "miracle glues" widely available on the American market. "Pliobond," a Goodyear product, sold by W. J. Ruscoe Co., Akron, Ohio, has performed quite satisfactorily and has the advantage of being soluble in acetone.) The cylinder bottom is then placed firmly on an outsize coverslip. When dry, the overflow of cement can be scraped away with a needle, and the coverslip trimmed to the edge of the cylinder. Bipartite cylinders are made with one extra sawcut. The cut surfaces are lapped smooth and in use are stuck together with stopcock grease (Steeman Nielsen 1933). No further support is necessary to hold the split cylinder together when filled as the cohesion of the enclosed water is adequate for this. Locating the split no closer than 1 cm above the bottom of the cylinder permits full use of a long-working-distance condenser and also permits rapid and easy pipette draining of the removable upper part.

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BOOK REVIEWS

Perspectives in Marine Biology edited by A. A. Buzzati-Traverso. Berkeley, University of California Press, 1958. xvi + 621 pp. illustrated.

"A scientist engaged in a piece of research, say in physics, can attack his problem straight away. He can go at once to the heart of the matter; to the heart, that is, of an organized structure. For a structure of scientific doctrines is already in existence; and with it, a generally accepted problem-situation. This is why he may leave it to others to fit his contribution into the framework of scientific knowledge."

Popper (1959)

In 1956 the Scripps Institution of Oceanography, under the auspices of the International Union of Biological Sciences and in collaboration with the U. S. Office of Naval Research, sponsored a symposium in marine biology with the objective of permitting "a discussion focussed on possible forthcoming fields of development in marine biology rather than on a survey of past accomplishments." The symposium was organized on a most generous scale and some 37 specialists in a wide range of subjects accepted invitations to contribute papers. These papers and their authors were the core of the symposium around which assembled a larger group of observers and others making a total of 183 participants. During the symposium itself the specialists, with selected collaborators, were placed in a series of idea-groups, each composed of as heterogeneous an assemblage of specializations as could be made up from the available people. These groups met at lunch and at other times to exchange views on selected themes, and it was expected that in the climate created by the plenary sessions when their papers were read and discussed, the interaction between specialists and these small groups might strike some sparks of creative thought from which would come some original and productive new lines of research in marine biology. Thus, whilst the papers presented might establish perspectives in marine biology as it existed before the symposium, and were to offer each author's own views of the avenues open before him, the idea groups were, by their explosive action, to blow away some obscuring material and open up new avenues.

The volume "Perspectives in Marine Biology" is the report of this meeting. Since the conception of the meeting was so vigorous, and since also, in the reviewer's mind, the time still is opportune to consider perspectives in marine biology, it seems appropriate to take this volume, not only for review, but also as *point de départ* for a discussion of such perspectives, of the value of this symposium in defining these particular perspectives, and of the value of symposia in general for such purposes.

The volume contains 41 papers, grouped in four sections, titled: Ecology (13 papers), Physiology and Biochemistry (12), Behaviour (4), and Genetics and Evolution (12). Most papers are followed by a record of some of the observations made by members of the audience, questions put by them to the authors, and the authors' replies. One might have expected that these discussion pages would have revealed the meeting-in-operation yielding the hoped-for results, but at once it must be said that such expectation is not fulfilled for, as has since been observed by Bullock (1956):

"The main strength and main weakness of the conference . . . derived from the large number of people and the great diversity of disciplines represented . . . . The advantages of this feature were felt by the members of these disciplines per se, *while the disadvantage was felt by those who hoped for some synthesis, some formulation, or some agreement on a finite set of perspectives on the future of marine biology."*

The papers of the ecological section[1] may be considered, according to the principal characteristics of each, in four unequal groups. The largest group contains the papers of Rae, Drach, Riedl, Thorson, Wilson, Yonge, Tonolli and Hardy, in which selected phenomena or systems are described, difficulties of investigation are discussed and suggestions are made concerning either equipment (Drach, Tonolli, Riedl, Hardy), methods and organization of research, (Rae and Thorson) or objects of research (Wilson, Yonge). The papers

[1] Rae, K. M. — Parameters of the Marine Environment
Redfield, A. C. — The Inadequacy of Experiment in Marine Biology
Zenkevitch, L. — Immediate Problems in the Development of Marine Biology
Drach, P. — Perspectives in the Study of Benthic Fauna of the Continential Shelf
Wieser, W. — The Particulate and the Comparative Concept in Marine Synecology
Riedl, R. — An Attempt to Test the Efficiency of Ecological Field Methods and the Validity of their Results
Thorson, G. — Parallel Level-Bottom Communities, Their Temperature Adaptation, and Their "Balance" between Predators and Food Animals
Wilson, D. P. — Some Problems in Larval Ecology Related to the Localized Distribution of Bottom Animals
Barnes, H. — The Future of Underwater Television
Yonge, C. M. — Ecology and Physiology of Reef-Building Corals
Tonolli, V. and L. — Irregularities of Distribution of Plankton Communities: Considerations and Methods
Bogorov, B. G. — Perspectives in the Study of Seasonal Changes of Plankton and of the Number of Generations at Different Latitudes
Hardy, A. C. — Toward Prediction in the Sea

of the other groups more or less reverse the approach. Barnes' paper is essentially technological, dealing as it does with underwater television and its uses. Redfield and Wieser deal primarily with general concepts. Finally, Zenkevitch and Bogorov deal with the general organization of marine biological research and with the matters to which it may be applied.

The papers of the Physiology and Biochemical section[2] fall into three distinct groups, of which the largest includes the papers of Baldwin, Bullock, Guzmann Barron, Szent-Györgyi, Kon, Arnon and Provasoli dealing with phenomena at the cellular and hormonal level. A second group, the papers of Pittendrigh and Brown are better described as biophysical-behavioristic-autecological, whilst those of the third group, Rodhe *et al.*, Margalef and Belser, are synecological. Essentially, however, all these papers are of the first, major class I have made for the ecological section, each (with the exception perhaps of the strictly biochemical papers of Baldwin and Szent-Györgyi) describing some phenomena or systems and discussing further work to be done on "problems," and at times dealing with instrumentation.

Of the papers in the Behavior Section[3], Thorpe's deals with general ideas. The other three (Watermann, Hasler and Miyadi) present accounts of particular work in this field and could be placed in the first of the classes described above with regard to the Ecological section.

Two of the papers (Buzzati-Traverso, Drach) of the section on Genetics and Evolution[4] don't belong there. Of the rest, seven (Loosanoff, Wieser, Novick, Lewin, Barigozzi, Kohn and Yonge) fall into my first class of descriptive papers leading to statements of kinds of research that might be done. One (Ray) is methodological and, with Rae, advocates the establishment of experimental marine animals. Another (Montalenti) deals with the mechanics of genetic systems and the last (Matzui) deals with histology.

PERSPECTIVE AMONG FACTS

There is moving at present a very commonly held opinion that something is wrong in the house of the marine biologists. It is said that the science is stagnant, that its practitioners have lost their way in a wilderness of descriptive material, that these workers have no navigational directive such as guided systematics when provided with the broad concepts of Darwinism. In such a climate of opinion, it is perhaps proper to make some massive effort to find these directives; but whether this is so and how we might go about it depends, in my view, on one's philosophy about science, its objects and its methods.

If your philosophy is of that kind, you may doubt that the physical world exists, more or less as it appears to us when we observe it, regardless of whether we are observing it or not. Such a position must have its special consequences with which, however, I propose not to deal. But most scientists hold a contrary view which applies also to the research workers studying the physical world, and to their institutions, instruments and equipment generally. It must equally apply to knowledge of the physical world, there being a one to one correspondence, virtually a synonymy, between each smallest feature of the physical world and the record of it. The world is a vast mass of information, most of which is relatively redundant for any particular purpose.

The position with respect to scientific theory is, however, quite otherwise, except as it would be if there were a supranatural observer, or if there might be life on other worlds and if beings there could observe us and know our thoughts; to these our formulation of ideas and our construction of theoretical models could be an aspect of our ethology as interesting to them as the behavior

[2] Baldwin, E. — Some Biochemical Problems in Marine Biology
Bullock, T. H. — Homeostatic Mechanisms in Marine Organisms
Guzman Barron, E. S. — The Regulatory Mechanisms of Cellular Respiration
Szent-Györgyi A. — Motion, Energy Transmission, and the Cellular Matrix
Pittendrigh, C. S. — Perspectives in the Study of Biological Clocks
Brown, F. A., Jr. — Studies of the Timing Mechanisms of Daily Tidal and Lunar Periodicities in Organisms
Kon, S. K. — Some Thoughts on Biochemical Perspectives in Marine Biology
Rodhe, W., R. A. Vollenweider, and A. Nauwerck — The Primary Production and Standing Crop of Phytoplankton
Margalef, R. — Temporal Sucession and Spatial Heterogeneity in Phytoplankton
Arnon, D. I. — Some Functional Aspects of Inorganic Micronutrients in the Metabolism of Green Plants
Provalsoli, L. — Growth Factors in Unicellular Marine Algae
Belser, W. L. — Marine Microorganisms: Some Generalizations concerning their Importance to Marine Life

[3] Thorpe, W. H. — Ethology as a New Branch of Biology
Waterman, T. H. — Polarized Light and Plankton Navigation
Hasler, A. D. — Perception of Pathways by Fishes in Migration
Miyadi, D. — Perspectives of Experimental Research on Social Interference among Fishes

[4] Loosanoff, V. L. — Challenging Problems in Shellfish Biology
Ray, D. L. — Some Marine Invertebrates Useful for Genetic Resarch
Wieser, W. — Problems of Species Formation in the Benthic Microfauna of the Deep Sea
Matzui, Y. — Aspects of the Environment of Pearl-Culture Grounds and the Problems of Hybridization in the Genus *Pinctada*
Novick, A. — Some Chemical Bases for Evolution of Micro-organisms
Barigozzi, C. — Genetic Systems in Sessile and Semisessile Organisms
Lewin, R. A. — Genetics and Marine Algae
Kohn, A. J. — Problems of Speciation in Marine Invertebrates
Montalenti, G. — Perspectives of Research on Sex Problems in Marine Animals
Drach, P. — A Few Remarks on Marine Biology, Animal Biology, and General Biology
Yonge, C. M. — Some Genetical Problems Presented by Sessile Coelenterates
Buzzati-Traverso, A. A. — Perspectives in Marine Biology

of animals is to us.[5] Such behavior is for us part of the data of the physical world and exists independently of our observation of it. But not so our theories and models, for they exist, for us, only with us; their currency depends on our communications, and their permanency on their correspondence, so far as it appears to us, with the physical world as we see it.

The relevance of these observations to the present review is as follows. When one speaks of perspectives, one should make clear whether one is speaking of the relations that *do exist* within the physical world, or of those that *may be established* in the conceptional world. For the former (which, as I have indicated includes knowledge of it) one may speak in a near-absolute sense. It is true that the view from each observation point may give a unique impression, but it must be possible by means of objective transformers to convert all views to the value of any selected one, and to do this as often and to as many base references as one might wish. Thus the nationals of a particular country might consider that the inventory of crustacean species of *their* country was the most important section of work to be done in crustacean systematics, but it should be relatively easy for scientists engaged on crustacean systematics to establish at any one time a more or less true perspective of knowledge of crustacean species of the world.[6] It should be possible to deal similarly with conflicting claims of specialists in different groups of organisms. It would seem to me that it would be a relatively simple matter (albeit a large task) to establish perspectives in this sense, addressing oneself to questions such as: What areas of the seas remain unexplored? What communities undescribed? What species inadequately identified and listed? What systems unanalyzed? The success of such an operation would depend on the comprehensiveness of the frame of reference against which the study was made. It is relatively immaterial that in some cases (*e.g.* in reviewing knowledge of zoogeographic areas) the most convenient frame of reference has such correspondence with the physical world as to be a model of it, for in fact, the correspondence of a theoretical model with the system it represents is of kind other than that of a frame of reference, such as a geographic map, with the physical world in space.

Considering the volume under review in this sense, the conclusion is inescapable that the symposium was not a success. It furnishes no clear or reliably comprehensive idea of what is known (or, reciprocally, of what we know needs to be found out) about areas, systems, processes, species, organisms or any other category of marine biological phenomena. This view is reinforced by a comparison of this volume with Walford's "Living Resources of the Sea" (Walford 1959) in which a much more systematic and successful survey is presented and perspectives of this kind truly established. The contributors to the volume under review are presented as being like the wise and blind men of India who from their several positions around an elephant formulated several quite different and incompatible accounts of what was presented to them. There is no account of the totality of marine biology; the interdisciplinary interaction failed to induce the formulation of one. Zenkevitch and Bogorov were both aware of this problem and both proposed comprehensive systems for planning marine biological research programs. Thorson too, and Wieser, with their pleas for comparative studies, pointed the way to perspectives. This disability seems to have impressed also Bullock who, in one of the most striking sections of recorded discussions (p. 184) observed:

> *"But I am deeply disturbed by the impression that one great area of ecology, or rather a general approach to biology, is being omitted, at least from the stated plans, though I am sure many of you fully appreciate it in principle, I mean the over-all quantitative accounting for each whole ecological system. Recognizing the objective of, and formulating the requirements for, a real evaluation of the amount of each main category of mass and of energy in the whole system, at a given time and as a function of time, would put us a long way ahead in our perspectives on the more detailed ecological questions involving named species."*

PERSPECTIVE AMONG CONCEPTS

Of course it may be said that the symposium was not intended to perform such a mechanical task. After all, making an inventory is a pedestrian —almost technological—rather than scientific occupation. Therefore let's consider a different set of perspectives. These will be such as we might find in the purely conceptual world: "the proportions in which the parts of a subject are viewed in the mind". Here we have no firm landmarks because the models are entirely of our own making, and of that there is no apparent limit. Here we are concerned with epistemological problems, with the methods by which we obtain knowledge and test its validity, and the systems in which we organize it. In this sense we find the most important contribution of the symposium, and the chief weakness of the published volume.

Let us dispose first of the latter—I refer primarily to the arrangement of the papers and the titling of the sections. Ecology is a broad subject which, in my view, includes with respect to the organisms it studies and from different viewpoints, such subjects as physiology and biochemistry on the one hand, and as behavior and genetics and

[5] I leave to one side the question of whether there might be some identity between man's psyche, that enables him to include himself within his world of observation, and some supranatural being.

[6] It is of course obvious that those of a chauvinistic attitude apply a non-objective scale.

evolution on the other. Physiology and biochemistry study certain life processes at particular levels, and if there should be a section for physiology and biochemistry there might well be sections also for biophysics, anatomy and other lines of research at other levels. But behavior and genetics are not of a different category, they do not comprehend the whole of the phenomena of living organisms; neither of them alone (nor the two together) provides a full account of reproduction, growth, distribution and variation.

Turning then, to the strength of the meeting, there were, I believe two main approaches possible. Firstly a review might have been made of methods of study, in an attempt to assess their efficacy and to discover (especially by reference to experience gained from the use of such methods on other material) the ways in which developments of these methods might be made. Secondly, a review might have been made of concepts of living phenomena to assess their adequacy, for which purpose the proper test is the power of prediction.

In the first of these approaches there is a rather barren bypath that leads to papers such as that of Barnes, and to much of what is in the papers of Drach, Riedl and Hardy. It is the ingenious engineer's approach which becomes obsessed with gadgets and often ends in scientific decadence. The longer course is in fact the main highway of science and hence the more exciting. Here we have Redfield's paper on experimentation, the debate on which at least opened vistas of decisions on deduction versus induction. Here we have one of the large problems confronting marine biologists—how to subdue their steadily mounting accumulation of descriptive record by, among other methods, rigorous testing against experimental results? And here too we have another basic principle of scientific method: the obligation that research has, in almost every sense, to prove itself by furnishing and verifying predictions, a subject referred to by Hardy, although there was a striking naïveté in his presentation, as though he believed that he was offering a novel feature to be found in such research. I suppose that no one can yet specify, conclusively and comprehensively, the characteristics of a complete science, and yet it would have been useful if this symposium had more assiduously pursued these two leads, in conjunction with consideration of aspects of the Zenkevitch, Bogorov and Thorson papers, even in exchange, if need be, for publishing the papers in this volume. How much, if at all, should there be of induction and of deduction? What relation between them? What predictions?

But this turns us to the second approach; what concept do we have of the part of the physical world that marine biologists study? We may think of it as an assemblage of individual organisms, or of individual communities, or as a single complex process of movement of material and energy. Some important ideas in this sense are current today. There is that large idea of basic production and of varying productivity. Rodhe *et al.* presented a nice account of some work in this field and Bullock (*loc. cit.*) made a plea for such an approach, but nothing much came of either. There is also the exciting idea of population dynamics which in a qualitative way was touched on by Margalef, and as far as I can find is mentioned as such only once (p. 615) in the volume. There is the idea of an ecological diagnosis of a species requested by Kinne (1958) at Drach's Roscoff Symposium in 1957 which, although not mentioned, was in effect touched on by Thorson. The broad idea of genetic systems and of evolutionary processes did receive much attention; in fact the liveliest debate (or at least the longest record of debate) followed Kohn's paper on speciation, but it was a debate characterized by the citation of particular evidence, and resembled the thousands of such debates that have taken place since Darwin.

Alternatively, we may adopt the comparative method and consider the appearance of similar organs or processes throughout a range of levels of organization, or of organizational forms throughout a range of environmental circumstances. Of the former there are the papers of Pittendrigh and Brown on rhythms, of Bullock on homeostatic mechanisms, and of Kon on enzyme systems; stimulating papers, but restricted and not of the scope to establish perspectives. Thorson's paper is an example of the latter. But what of osmo-regulation throughout the aquatic biosphere? or of growth regulating processes? or biotic relations generally? and of the perhaps profitless debate about density-dependence and density-independence? to mention only a few of the major ideas current today that might have been put into perspective.

Thus, I would conclude that an opportunity has been lost, and the possible effect of the contributions reduced, by the failure to make a creative arrangement of these papers. This feature manifests itself within each section.

DISCOVERIES IN SCIENCE

Scientific method consists of various elements. The observations of free or controlled objects of study, the accumulation, analysis and interpretation of the data from such observations, the setting up of hypotheses and theoretical models as frames for planning observational programs, and the construction of logical method to control and guide the foregoing. For most of these it is possible to seek to establish or agree on perspectives of one or other kind, and I have, in the foregoing pages, attempted to assess the value of the volume under review with respect to these. But beyond these, there is another element for which it would scarcely be possible to establish any perspective. I refer to intuitive apprehensions of relation and significance. Obviously these cannot be forecast, for they are the principal element of the unpredictable in science; once made, their result is indistinguishable from all other enlargements of our understanding, by whatever way they may have come. Such contributions are important; often the problems solved

in this way are the most critical in their field. But can a field of science be characterized by the frequency with which such discoveries are made in it? Or are there phases in the history of each science in which such discoveries are made with greater frequency than in others? Are there times in which the practitioners of a science move, as though inspired, with perfect poise, disregarding redundant signal, recognizing only the significant, unerringly achieving result after result? Such periods do seem to occur, and manifest themselves as famous "schools". They cannot be deliberately arranged, they arise I believe out of fortunate conjunctions of mind and personality and circumstance. For, despite the intellectualism of its method, the energy of scientific research derives from personality, made effective by circumstance. And thus, we have a special, last view of our science, in which perhaps the concept of perspectives is no longer valid, for in it there are no scales of space or time or subject, but only of value, which is perhaps not a measure to be used in science.

Intuitive discoveries cannot be arranged, nor can they be forecast. It would be reasonable, although contrary to common and dramatic usage, to hold a definition of discovery that excluded from its connotation all cases of prediction of what was discovered, and to hold that any predicted result of a "discovery" was only the completion of a structure of which the plan was already drawn. There are those who hold such a view and who consider that only the making of discoveries, in their narrow sense, is true science. Others go along with them only to the extent of agreeing that intuitive discoveries are the finest fruits of science, but pointing out that equally part of science are its leaves, stem and roots, and that some of the poorer fruits are not to be despised.

Symposia as a Method of Science

Now, in the matter of symposia, one's attitude to science (in the sense of the preceding paragraph) must make a lot of difference to one's expectations from such meetings, and to one's arrangements for them. It would seem to me that those who hold the first—the "pure"—view above cannot with consistency set scientific objectives for a symposium. They can only hope that the occasion they create might fortuitously provide someone with some happy insight. It is a question how far they would be willing to concede that they could "arrange" the propitious aspects of the occasion, and thus increase the chances of fortunate outcome. Since they seem to me to be of the nature of mystics, as well as anarchists, I must suppose that they would be ready to resort to abracadabra, charms, incense and other apparatus (their homologues, of course, in the scientific world) to induce favorable manifestations. But for them perspectives are scarcely a real proposition and even less a possible outcome of a symposium.

For those to whom science is the whole tree and not merely its best fruits, a symposium is a scientific operation that can be planned and conducted to produce scientific results of various kinds. Among these results the achievement of agreement on standardization of terminology equipment and method is of first-rank importance and one for which symposia are, in certain circumstances, especially well-fitted. Another result that may come from a symposium is agreement on a common plan. Perhaps the most appropriate objective of a symposium is establishment of perspectives of the first kind described above and temporary agreement with regard to those of the second. Whether such an objective is achieved at a particular symposium will depend largely on the original statement of its plans and on the arrangements made for it.

It is my view that in recent years a technique of symposia has emerged to replace to some extent the older type of scientific gatherings. In this technique particular objectives are set and arrangements made to canalize, direct and make maximum use of the exchanges made possible by the symposium. To some certainly, such deliberate planning and such management is abhorrent; but it is equally clear that the validity of this approach is steadily gaining acceptance—which of course is no final test since one might be watching only a passing phase. However, considering the growing embarassment of the scientific world from its steadily lengthening schedule of meetings, to which each year are added more and more official meetings at which scientists must assist, it is opportune to enter a plea for the application of some simple scientific principles in the planning and conduct of scientific meetings.

Buzzati-Traverso, the editor of this volume and moving spirit of the Symposium, has written a final, post-symposium chapter which he says is not a summary or synthesis of the papers presented, but which, nevertheless lists ideas and suggestions presented in those papers. The list seems unfortunate: its wording is that of the pious resolutions of large congresses; rationale is apparent neither for the selection of items nor for their formulation. To take one almost at random, No. 10 is: "The study of the spectacular migrations of eels, salmon, and other fishes and of their causative agents ought to be studied more intensely than is done at present." Why? Why the spectacular migrations more than any others? Why migrations more than any other feature of the behavior of marine organisms? However, we must be grateful for the few paragraphs that follow this list. In the sense of perspectives they are perhaps the best part of the book; they are written with the easy command of fact and idea that characterises classical writing in biology.

To sum up, I have suggested that perspectives in marine biology might have been identified, or agreed upon, in the following ways:

1) by establishing an inventory of our knowledge of marine biota and comparing this with what, as far as we can see at present, must be the complete schedule of such information immanent in the physical world;

2) by reviewing our methods of study, and attempting to assess their efficacy for the task of completing that description and to discover the ways in which these methods might be developed;
3) by reviewing our concept of living phenomena to assess its adequacy for the purposes of prediction.

I have referred to a further source of discovery, namely the intuitive, and have expressed the opinion that no perspectives can usefully be established with respect to these.

And I have concluded that this volume does not establish any of these perspectives, although because of the wealth of its material, and of the importance of its idea, its existence may lead its readers to employ the methods I have described and, by more systematic study, to establish perspectives for themselves.

Finally, I have entered a plea for a more scientific approach to the planning and conduct of scientific meetings.

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Russian-English Glossary of Hydrobiology. Editor: Frank L. Sinclair. Compilation: Sonia Novek. Interlanguage Dictionaries. New York 1958. pp. 1–113. $7.50.

In bilingual technical dictionaries accuracy is hard to achieve even with the most painstaking scholarship. In this publication not only has there been no apparent effort at scholarship but naïve disregard of the simplest rules of glossary making has produced a collection of very misleading and inaccurate information. Unfortunately, younger students and those not trained in linguistics or biology may incorporate definitions from this publication into their work. The major defects are stated in the following paragraphs in an effort to avert this among beginners in the study of the Russian biological literature. It is assumed that old hands will not take the publication seriously.

A large proportion of this glossary seems to be a mechanical inversion of Smirnov's English-Russian Hydrobiological Dictionary. Conservatively estimated, this procedure renders one fourth of the entries either misleading or categorically incorrect. Standard procedures of punctuation and index subordination have not been used and the glossary is internally inconsistent in the application of those systems which are used. Standard abbreviations (bot., orn., anat., etc.) have been omitted in about half the entries where they apply. Many of the Russian and English vernacular names of animals and plants as well as their scientific equivalents are out-of-date, misapplied, inadequately defined, or simply wrong.

Mechanical inversion will not produce a Russian-English glossary from an English-Russian base for the same reason that inversion of entries in a simple English dictionary does not lead to a logical result. The entry "dog—noun, a mammal" is correct but the entry "mammal—noun, a dog" does not follow. If the vocabulary of Russian were congruent with the vocabulary of English, *i.e.* if every Russian word had a coextensive equivalent in English, it would then be possible to set up an English-Russian glossary which could be mechanically converted to Russian-English. Whether or not there are any words in Russian which are exact synonyms of English words is a debatable linguistic problem. In any case, at the practical level such synonyms are so few that the bilingual glossary of this sort must take the form of index entries followed by descriptive material, just as does a one-language dictionary. The following examples are quoted from the book under review:

(1) ZEMNOVODNOYE newt (*Diemyctylus viridescens*)
(2) DELENIYE fission

Entry (1) is the neuter form of an adjective very nearly synonymous with the English adjective "amphibious," and this entry is just as meaningful as "feathered—noun, robin" would be in a standard English dictionary. Entry (2) is well defined in Callaham's standard technical dictionary as "n. division, dividing, sharing; graduation; indexing; parting; dial; partition; DELENIYE KLETOK (biol.) fission; . . . ."

Internal inconsistency of punctuation makes it impossible to interpret correctly many entries.

(3) GLADKIY glabrous, smooth
(4) KATUSHKA coil; ramshorn or trumpet snail (*Planorbis* sp.)
(5) GLINA clay; puddle

Entries (3) and (4) correctly use the conventional system of separating synonyms by commas and words essentially different in meaning by semicolons (glabrous is a synonym of smooth, coil means a coil of rope, and trumpet snail is different in meaning from coil). But entry (5) uses a semicolon between "puddle" and "clay," thereby implying a difference in meaning even though "puddle" refers to the same substance as clay in this instance and not to a puddle of water on the ground.

Standard abbreviations are included or omitted at random.

(6) DEL'FINOVIY dolphin
(7) GOLEN' (ent) tibia

(8) VYNOSYASHCHIY (anat) efferent

Entry (6) does not indicate whether a fish or mammal is intended. Although English uses "dolphin" to apply to both, this Russian form applies definitely to Delphinids, members of the mammalian family Delphinidae. Entry (7) is used to refer to the shin bone in many groups; it very commonly refers to the tarsus in birds and is by no means restricted to the insects as here indicated. Entry (8) is a participial form of a verb with broad application outside the highly restricted anatomical reference here indicated.

Plant and animal names make up about one third of the glossary and about 80% of these entries include scientific names. Obtaining accurate correspondence between vernacular and technical nomenclature in a bilingual dictionary is extremely difficult due to the constant taxonomic re-working of many groups, differences in attitude toward classification, the slow but constant evolution of vernacular names, and the numerous dialect and local differences in language areas as extensive as the Russian and English speaking countries. In this field lexical errors and lack of clarity are to be expected, but for this very reason it is of greatest importance that these errors be reduced to the minimum by some uniform system of approach. This glossary uses no system in presenting plant and animal names and the result is complete confusion. Even the simplest entries involve misunderstanding of the most fundamental concepts of language and taxonomy.

(9) EVFAGUS (USA) grackle (*Euphagus* sp.)

Entry (9) is a simple transliteration of a technical generic name. It is not a Russian word although treated as such along with many other similar simple transliterations. "Grackle" properly refers to species of the genera *Quiscalus* and *Cassadix,* not to *Euphagus,* which includes the rusty blackbird and its close relatives. The proper Russian term for the American blackbird and grackle group is ZHELTUSHNIK. The term ZHELTUSHNIK does not appear in the glossary although various New World blackbird species to which it refers are included under the transliterated form of their Latin names. Refer again to entry (1), which not only exemplifies the result of mechanical inversion but also misunderstanding of the relationships between Eurasian and American animals and their nomenclature. "Newt" commonly refers to any of several species of small salamander, especially those of the genus *Triturus.* Although the species cited in entry (1) (*D. viridescens*) does not occur in Eurasia and does not have a pure Russian vernacular name, several other species of the same genus are widely distributed in Eurasia and referred to in Russian as TRITON. The Russian equivalent of "newt" therefore, is TRITON, each word referring to the genus involved and not to a particular species. In this glossary one does indeed find this equivalent indexed under TRITON. One wonders, therefore, why the entries were not checked against one another, the discrepancy noted (*i.e.* "newt" carried under both ZEMNOVODNOYE and TRITON), and corrected. One explanation in this particular case might be that the out-of-date generic name *Diemyctylus* is used in entry (1) whereas an effort to use the correct contemporary generic term (*Triturus*) was made in defining TRITON (unfortunately typographical error brought it out "Tritutus"). In any case, *why* such an extraordinary collection of misinformation was put out is relatively unimportant. The important consideration is to avoid having it copied into future glossaries in this field, which we hope will be forthcoming in due course.

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